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HabCARES

Proceedings of a Workshop on the Science and Management for Habitat Conservation and Restoration Strategies (HabCARES) in the Great Lakes

Kempenfelt, Barrie, Ont.
November 1994

Comptes rendus d'un atelier sur la science et la gestion des stratégies de conservation et de restauration des habitats (HabCARES) dans le bassin des Grands Lacs

Kempenfelt, Barrie, Ont.
Novembre 1994

Special Editor/Directeur scientifique spécial

J.R.M. Kelso
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Introduction to the International Workshop on the Science and Management for Habitat Conservation and Restoration Strategies (HabCARES)

J.R.M. Kelso and C. Wooley

Background

Society can make three choices that affect future conditions for ecosystems; these same choices apply to the Laurentian Great Lakes. Society can (*i*) continue some rate of destruction, (*ii*) establish a policy of no net change or conservation of the current state, or (*iii*) use the no net change or conservation option as an interim measure after which repair exceeds net destruction. The governments of Canada and the United States, through the Great Lakes Water Quality Agreement and its amendments, recognized that rehabilitation and enhancement of their boundary waters was required and have provided guidelines for implementing restoration.

Direct action to conserve, restore, enhance, and rehabilitate (see Bradshaw (1996) for context of these action terms) has been encouraged not only by federal, state, and provincial legislation but also by international (e.g., Lake Superior Binational Program, remedial actions in interconnecting channels of the Great Lakes) and public (e.g., Lake Superior Cleanup, fish restoration actions by sport fisher groups) initiatives. Only informed decision making will result in actions that are effective and economical. Some, hopefully most, people believe that it is essential to have both the legislation and well-conceived management approaches founded in sound science. Cullen (1990) aptly described the relation between science and management as being turbulent. At least, if actions and approaches are applied with good scientific method and thoughtful biological and ecosystem assessment, future conservation and repair actions will benefit.

Purpose for ecosystem repair should be provided by objectives (White 1991), and these were articulated for the Great Lakes ecosystem and its fish communities in Annex 1 of the 1987 Protocol to the Great Lakes Water Quality Agreement and in the Joint Strategic Plan for Management of Great Lakes Fisheries. Lake-specific ecosystem objectives to maintain and restore physical, chemical, and biological integrity also have been developed. Hartig (1993) and Koonce (1994) made an attempt to ensure that Great Lakes objectives are compatible. The evolved cooperative process in the Great Lakes ecosystem provides some assurance that the focus is upon objectives.

Linkages between physical habitat and ecosystem performance are only partly understood and the documentation of the benefits from past actions to the ultimate benefit of ecosystems is limited. Because ecosystems as we recognize them are not isolated but are interconnected subsystems of a larger landscape, the status of theoretical science and the assessment of the benefits of actions is far from robust.

Unfortunately, the role that habitat conservation and repair can play in achieving ecosystem objectives is not always considered. Many resource management strategies (e.g., introductions from hatcheries and harvest regulation) can be varied but require both continued assessment and justification. Physical habitat of ecosystems is or should be constant or changing in a predictable manner (i.e., through senescence). Consequently, habitat repair, if it leads to achieving ecosystem goals and is done well, has a one-time cost and provides a lasting contribution to long-term action plans. Clearer understanding of the effect of habitat alteration and the role that habitat change can play in achieving ecosystem objectives is mandatory.

The costs of ecosystem repair are high. These costs alone demand better accounting and understanding of benefits (see Kelso and Hartig (1995) for recent examples of methods and costs for actions in the Great Lakes).

The HabCARES process

The International Workshop on the Science and Management for Habitat Conservation and Restoration Strategies (HabCARES) continues the series of symposia supported and partly sponsored by the Great Lakes Fishery Commission and published by the *Canadian Journal of Fisheries and Aquatic Sciences*. Early symposia documented human impact on the Great Lakes and the severity of environmental perturbations, including alteration of habitat through urban development and eutrophication. These proceedings included Salmonid Communites in Oligotrophic Lakes (SCOL) (J. Fish. Res. Board Can. 29(6), 1972), Percid International Symposium (PERCIS) (J. Fish. Res. Board Can. 34(10), 1978); Sea Lamprey International Symposium (SLIS) (Can. J. Fish. Aquat. Sci. 37(11), 1979), and the Stock Concept Symposium (STOCS) (Can. J. Fish. Aquat. Sci. 38(12), 1980). Two other proceedings, Assessment of Stocks and Prediction of Yield (ASPY) (Can. J. Fish. Aquat. Sci. 44(Suppl.2), 1987) and the Large River Symposium

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(LARS) (Can. Spec. Publ. Fish. Aquat. Sci. No. 106, 1989), focused more on management of aquatic resources.

These symposia used a steering committee and a workshop-type format to successfully meet their objectives; we used their method. In the workshop at the Kempenfelt Centre, November 14–18, 1994, we sought to assess and synthesize the understanding of the linkages between habitat, production, and structure of aquatic and wetland communities, identify successful habitat restorations and enhancements, identify and fill important gaps in scientific knowledge, and provide recommendations for resource managers to effectively conserve, restore, and enhance aquatic habitat.

Forty-three background papers were prepared in advance of the workshop and seven discussion groups responded to challenges developed by the steering committee. This supplement includes the original research papers, case history papers, and perspectives either invited or developed at the workshop that survived peer review.

The challenge

In grappling with fundamental questions on how the environment affects animal activity, Fry (1947, p. 59) suggested that although our present understanding may be flawed, it needs to be expressed "for there is a great deal more value in having things corrected than there is in never stating them; the road to truth lies much through argument." These proceedings, particularly those papers that tried to integrate information or synthesize ideas, provide a good basis for argument. Hopefully, freshwater science, which now proceeds in an atmosphere of severe fiscal restraint, at least in Canada, can still address those uncertainties that impede successful ecosystem conservation and repair.

This supplement may provoke those who routinely promote, market, or implement habitat improvement techniques or technology with little or no evaluation of their relation to ecosystem performance. Minns et al. (1996) and Lester et al. (1996), particularly, indicate the process and rigour required to detect responses to change in a way that will benefit our ability to conserve and repair ecosystems. It is essential, in our view, to maintain an independent and continuing scientific process whereby remedial techniques are evaluated and uncertainties addressed; if society fails to support such programs, expensive and ineffective ecosystem and repair initiatives will inevitably result.

If habitat is "managed," it is axiomatic that all types of habitat needed for a species to complete its life cycle are important. These proceedings help focus on habitat features that man has affected most. The lack of initiatives that were successful in restoring or repairing aquatic ecosystems or its properties is, however, disconcerting. It may be simply that rehabilitation and enhancement efforts are too recent to yield results. Nevertheless, we suggest that society's ability to protect and rehabilitate will be least where scientific uncertainty and sampling variability are greatest.

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Underlying principles of restoration

A.D. Bradshaw

Abstract: The term restoration is used in many ways; however, it normally implies return to an original state. In ecological restoration, it should be thought of as applying to whole ecosystems. It must be remembered that options, such as rehabilitation or replacement, exist that may be more practicable than restoration. The components of restoration are the chemical and physical aspects of the habitat and the species themselves. Each of these may require specific treatment, but natural restorative processes should be used wherever possible; in fact, natural processes may be sufficient once the degrading influences have been removed. Because the process of restoration is progressive, the criteria of success are not easy to define. The most important point is that ecosystem development should be on an unrestricted upward path. From this, it follows that successful restoration is a serious test of our ecological understanding.

Résumé : Le terme restauration est utilisé dans plusieurs sens, mais il suppose normalement un retour à l'état initial. Dans le domaine de l'écologie, il faut voir la restauration comme s'appliquant à des écosystèmes complets et se souvenir que d'autres solutions, comme la rehabilitation et le remplacement, peuvent être plus réalistes. La restauration vise à la fois les aspects chimiques et physiques de l'habitat et les espèces elles-mêmes; chacun de ces volets peut exiger des mesures particulières, mais il faut autant que possible se fier aux mécanismes naturels de restauration. En fait, si on a éliminé les sources de dégradation, ces mécanismes sont souvent suffisants. Comme la restauration est un processus progressif, il peut être difficile de fixer des critères de réussite. Il faut avant tout se rappeler que l'écosystème doit se développer sans entrave dans le sens d'une amélioration. La réussite d'une telle opération met à rude épreuve notre compréhension de l'écologie. [Traduit par la Rédaction]

Introduction

There is a tendency for individual groups involved in the practical aspects of restoration to pay little attention to what others are doing, or have done. The reason is usually that they feel that their problem is special and has little connection with others, because of climate, terrain, species, or any of the many other ways one community can differ from another. Yet the strength of modern ecology is that it has been able to produce underlying principles of general application.

In restoration ecology it is clear that general principles are developing that are applicable widely, no matter whether the subject is the restoration of tundra, tropical forest, lakes, or farmland. Because the HabCARES workshop is mainly about aquatic systems and this paper is by an ecologist whose main experience is in terrestrial systems, the challenge is to show that generalizations are possible and can provide valuable guidance to restoration practice.

What is restoration?

We must be clear what is being discussed. Although words can change their meaning, it is important to examine what they have meant until recently (here using Oxford English Dictionary; Fowler and Fowler 1971). The relevant definition of *restoration* is "the act of restoring to a former state or position ... or to an unimpaired or perfect condition." To *restore* is "to bring back to the original state... or to a healthy or vigorous state. There is both the implication of returning to an original state and to a state that is perfect and healthy. This seems to be the way in which we continue to use the word on both sides of the Atlantic.

Rehabilitation is defined as "the action of restoring a thing to a previous condition or status." This appears rather similar to restoration, but there is little or no implication of perfection. Indeed in common usage, something that is rehabilitated is not expected to be in as original or healthy a state as if it had been restored.

Remediation is the act of remedying. To remedy is "to rectify, to make good." Here the emphasis is on the process rather than on the endpoint reached.

Reclamation is a term used by many practitioners, especially in Britain but also in North America. It is defined as "the making of land fit for cultivation." But to reclaim is given as "to bring back to a proper state." There is no implication of returning to an original state but rather to a useful one.

Replacement is, therefore, a possible alternative option. To replace is "to provide or procure a substitute or equivalent in place of" (although an alternative meaning is to restore).

Mitigation is a word often used when restoration is considered. It is important to note that it is nothing to do with restoration. To *mitigate* is "to appease... or to moderate the heinousness of something." So although mitigation can be an outcome of restoration it is a separate consideration.

Since the word restoration has been adopted for the title of this workshop, it will be used as the point of reference, despite its troublesome perfectionist implications (Francis et al. 1979).

To what are these words applied?

This problem must be addressed because here is where perhaps the greatest confusion lies about what we are doing. From our biological point of view we can apply it to ecosystems, habitats, communities, species, water or soil quality, or some other

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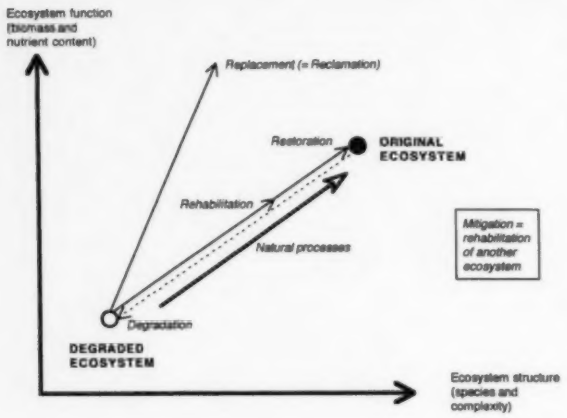
Fig. 1. The several different options in remediation work.



characteristic of the degraded or damaged area. All these are different, and therefore, their use has specific implications.

The word *ecosystem* covers the biological and nonbiological elements occurring together in a particular area. So it is all inclusive. However, because "system" is included, there is an emphasis on the overarching functions and interactions of these elements. So when the restoration of *ecosystems* is being referred to, the suggestion is that we are particularly interested in the restoration of the fundamental processes by which ecosystems work. This has been well argued by Cairns (1988).

It is common now to talk about *habitat* restoration; it is in the title of this workshop. Because habitat refers just to the place where organisms live, it tends to imply less than ecosystem. Its use, therefore, puts more emphasis on the restoration of place than of important ecological functions. We can also talk about restoration of *communities* or of *species*. In this case the emphasis is on just the plants and animals occurring in a particular place, or on a single species.

We also talk about restoration of *quality*. This is particularly true in discussions of soil or water restoration, perhaps because the species in these habitats are multifarious and their individual occurrences difficult to predict; therefore, the implication is different. It is the perceived attributes of what is in an area, or of a component of the environment, that are considered to be important. To what is referred depends on the particular situation; it could be either an important factor, such as biological oxygen demand or level of contaminants, or a derivative of well being such as species diversity.

Whatever we may think deserves attention, our intention should always be to focus on the restoration of functions, of processes, because without this the communities of organisms in which we are interested cannot persist. Our ultimate aim should be the restoration of the whole ecosystem, even if we sometimes emphasise some particular component or attribute (National Research Council 1992, Ch. 1).

Options in restoration

There are clearly many attributes to an ecosystem. These can usefully be simplified into two main components: structure and function. What has happened in a damaged ecosystem can then be represented graphically with these components as the two axes (Bradshaw 1987*a*) (Fig. 1). Both components will have suffered and will have to be restored. Rehabilitation, in which progress has been made but the original state not achieved, and reclamation, to something different, can be represented on the same figure.

This clarifies our options. In particular it points to the fact that restoration may not be easy. It may be possible, perhaps, to restore the functions fairly completely, but to achieve the original structure may be more difficult. This may not be so true in an aquatic ecosystem where, because of the smallness and consequent mobility of the individuals, the rate of reestablishment of populations can be rapid, but it will certainly be true in a forest ecosystem where the full age structure may be impossible to achieve in less than 500 yr. It may not be possible to achieve an original soil profile in less than 5000 yr, although the biological functions of a soil can perhaps be restored in less than 10 yr.

So in many situations, true restoration may be unrealistic. It may also be impossibly expensive. So we should realise that rehabilitation and replacement can be proper options. Both these alternatives, by offering something different, may provide an endpoint that is more valuable than what was there in the first place. Replacement is a particularly interesting option since it may allow restoration of a component, such as productivity, to a higher level than existed previously. In the heavily developed agricultural land of Britain, sand and gravel workings left to fill with water have contributed enormously to the diversity of wildlife and landscape in many areas. This is valuable reclamation; however, it is not true restoration although there may be restoration of particular attributes such as biodiversity.

It is, therefore, very important that when any work is undertaken, the different options and what they each might involve are clearly worked out and understood. Figure 1 can provide useful guidelines. The endpoint of full restoration, although it may seem ethically the most justifiable and, therefore, the most obvious to adopt, may in fact not always be the most sensible in practical or biological terms.

Components of restoration

To judge what is worthwhile attempting it is necessary to appreciate what it involves. In essence, no matter what ecosystem is being tackled, once the damaging process has been controlled, the crucial characteristic of any intervention is that it should relieve those factors that are restraining the redevelopment of the ecosystem required. Obviously this can involve many different elements, depending on the ecosystem and the degradation that has occurred.

Essentially three matters will need attention: (*i*) remodelling the physical aspects of the habitat; (*ii*) remodelling the chemical aspects, nutrients, and toxicity; and (*iii*) replacing missing species or removing undesirable exotics.

Exactly what is required will depend on what is wrong. For instance, acid land left after coal mining will require liming; raw inert materials left to be soils will require nutrients; lakes overcharged with phosphorus may require mud pumping; lost species may require reintroduction. There are now handbooks as well as papers on all these and other problems (e.g., for land,

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Coppin and Bradshaw 1982; Lyle 1987; Schaller and Sutton 1978; Williamson et al. 1982; for water, National Research Council 1992; Ryding and Rast 1989; for the Great Lakes, Francis et al. 1979). It is possible rationalize what is to be done (e.g., for terrestrial habitats, Bradshaw 1987*a*; for lakes, National Research Ccouncil 1992, Ch. 4). Attempts are now being made to put this rationale into logical decision trees (Maguire 1988). It is essential to identify the controlling factors that will not ameliorate naturally and then address these first.

Use of natural processes

These recommendations may suggest that each fault or deficiency has to be addressed if restoration is to be achieved. Yet we all know that, in the Great Lakes region, the preexisting vegetation and soils were repeatedly destroyed by the great ice sheets that covered much of North America. When these retreated, natural processes were able to build up ecosystems to their present day complexity of structure and function. The different processes, covered by the omnibus term "primary succession," have been well described recently (Miles and Walton 1993). These same processes are visibly at work in the secondary succession that follows present-day disturbances, whether in old fields, tropical forests, or other situations (Gray et al. 1987). They are processes of considerable power; they can bring about major changes in time scales as brief as decades and are particularly applicable to large ecosystems such as the Great Lakes.

With such a series of natural processes that can be harnessed to help restoration, we have to decide what part they should play in our work. It should be axiomatic that they should be used wherever possible, firstly because they cost nothing in themselves (although they may cost something to initiate); secondly, they are likely to be self sustaining because they originate from within nature (although they may need nurturing in some situations); and thirdly, they can be used on a large scale. Although it is clear that natural processes can eventually achieve full restoration, some may take a long time and need to be assisted. It is not possible to describe all the ways in which natural processes can be used, but some illustrations can be made.

Physical problems

Many degraded soils and deposited materials are compacted and have a high bulk density. Yet the changes that take place naturally on glacial moraines (Crocker and Major 1955), as well as on coal waste heaps and elsewhere, show that radical changes can be brought about by the growth of vegetation, the incorporation of organic matter, and the activities of soil fauna and flora. However, in some seriously compacted situations, natural recovery is so slow that mechanical treatment is necessary. In aquatic systems, physical treatments are widely undertaken.

Nutrient problems

One of the commonest problems of degraded terrestrial environments is lack of nutrients, particularly nitrogen. The soil nitrogen capital, normally at least 1000 kg $N \cdot ha^{-1}$, can be rebuilt up by means of fertilizers, but this is expensive and involves returning many times. It is much simpler to introduce legumes, such as white clover *Trifolium repens*, which can accumulate nitrogen at the rate of 100 kg $N \cdot ha^{-1} \cdot yr^{-1}$. However, calcium and phosphorus levels must be sufficient to maintain the growth of the clover (Roberts et al. 1982), although N-fixing species can often be chosen that do not have as special nutrient requirements as clover. By contrast, nutrients such as phosphorus cannot be conjured out the air and will remain deficient if not added.

In aquatic systems the problem is usually excess of nutrients. Once inputs into flowing systems are stopped, recovery is usually rapid. But this does not occur so readily in lakes. For lakes of limited size the removal of the nutrient-rich bottom muds may be possible. In other situations a totally different approach, using natural ecological processes that involve the manipulation of phytoplankton by manipulation of the zooplankton (Moss 1992; Hosper and Meijer 1993), can be more effective. The fact that assisting the growth of protective macrophytes or even the provision of bundles of twigs, to provide safe sites for the zooplankton, is effective, challenges our understanding of the mechanics of the freshwater ecosystem. Unfortunately, the size of the Great Lakes make both these approaches impractical; natural dispersal and loss may be the only answer.

Toxicity

This can be one of the most intractable problems, which natural processes by themselves cannot easily overcome, as witnessed by the persistent degraded and often completely bare areas contaminated by heavy metals in many places in the world (Ernst 1974). Yet restoration of the northern deciduous forests destroyed by the nickel smelters at Sudbury, Ont., illustrates both the problems and possibilities (Gunn 1995). Earlier work suggested that the combination of acidity and metal toxicity could only be answered by the use of metal-tolerant grasses. However, once the acidity is relieved by liming, the metal becomes less available and trees, which root through the surface soil into the less polluted horizons below, can be planted. Once such trees establish, the development of the ecosystem takes a new direction. Surface conditions are ameliorated sufficiently for natural recolonization to occur. In the end, elevated metal levels may remain, but a fully functional forest seems certain to develop. On a smaller scale a vigorous grassland ecosystem has been developed on lead–zinc mine tailings following an initial stimulus of sewage sludge and fertilizers (Johnson et al. 1976).

In aquatic habitats, once the toxic input has ceased, natural processes can lead to recovery even where the toxicity defies treatment. This is well demonstrated by the progressive reduction in metals in the Mersey Estuary that has occurred since inputs have been reduced over recent decades (National Rivers Authority 1995). Acid rain can be a serious problem because whole catchments are affected. To reverse the effects, liming of lakes has been carried out, but such localized treatment has usually had only short-term effects. The logical answer is to treat the source of the problem and lime the catchment rather than the lake. Work on this has so far been very promising (Howells and Dalziel 1992). It is important to note that except for liming and reintroduction of missing fish species, everything else can be left to natural processes.

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Species

Because of the dispersal powers of many species it is easy to fall into the trap of thinking that natural processes can be relied on for all species. In terrestrial situations, if rapid establishment is required, sowing of the main plant species is always essential. It is then often presumed that other species will arrive on their own. But studies of the recolonization of chemical wastes over the last 100 yr show that several appropriate species are missing because their nearest populations are too far away (Gray et al. 1994). The herbaceous species of woodlands are notoriously poor at dispersal (Peterken 1974); therefore, it can be crucial to introduce the missing species by artificial means (Francis 1993). The comparisons made between intervention and leaving natural processes alone to achieve recovery at Mount St. Helens are particularly interesting (Franklin et al. 1988); intervention certainly leads to more rapid recovery, especially where destruction of the habitat has been most complete.

In aquatic systems the situation is different. Fish, of course, will often need transfer. But most of the important species are microscopic and easily dispersed. Natural dispersal processes are, therefore, usually effective, especially in streams and lakes where substantial transport processes exist. This may not be true, however, for new isolated water bodies. In one of the earliest and very successful attempts to create a new aquatic system for the conservation of wildfowl from a gravel pit, there was no need to introduce the wildfowl, but the water body was inoculated with aquatic plant and animal species by bringing in species-rich mud (Harrison 1974). This is now recommended practice (Andrews and Kinsman 1990). Note that it is inoculation that is suggested, not full-scale planting, since natural processes of species establishment and spread will take the developing ecosystem on to its mature state. The removal of species, usually of alien introductions such as the sea lamprey (*Petromyzon marinus*), is another problem altogether, unfortunately often impossible to rectify.

Engineering

All this leads us into the whole subject of ecological engineering (Mitsch and Jorgensen 1989) sometimes called bioengineering (Schiechtl 1980). The discipline is much wider than the restoration we are considering here, being described as the techniques of designing and operating the economy with nature (Odum 1989). But within it are many provocative examples of how ecological processes can be harnessed specifically for the purposes of restoration, particularly in civil engineering situations.

In any restoration situation it is important to become fully aware of the natural processes already occurring. This may mean detailed studies of primary succession in the damaged area or in analogous areas. The detail is important, as a mere record of species colonization may tell very little. In both aquatic and terrestrial situations it will be valuable to understand matters such as the origins of the immigrating species, the part played by safe sites for species establishment, the changes occurring in soil or water fertility and in microorganisms, and the effects of species interactions. It can be informative to study the factors that appear to be preventing succession (Gemmell 1975). There is a complementarity between academic and practically oriented ecological studies; this is discussed later.

The possibility of doing nothing

The contribution of primary succession and natural processes introduces an alternative possibility, the extreme option of actually doing nothing. This can be seen as the negation of restoration. If, however, natural processes of primary or secondary succession are powerful, they may be able to do all that is necessary. Certainly the forested fields of New England are witness to the power of old-field succession.

If restoration is used in a wide sense to include the restoration of biodiversity, then untreated areas may have an important place in the different strategies of restoration. In Britain, disused quarries are now recognised as being important additions to the countryside because, in their unrestored state, they provide havens for species that find it difficult to survive in the managed agricultural countryside (Ratcliffe 1974). Restrictions on ecosystem development can, indeed, be an advantage for some species.

Similarly, young lakes can be important. Gravel pits have allowed the development of previous threatened floras and the spread into Britain of the little ringed plover. In Indiana, strip mine pits and ponds have had an important role for wildlife, sufficient to make it important to develop methods of modifying them, but not destroying them, to increase their wildlife potential (Willard 1988).

The criteria of success

How far, then, should intervention go? Purists, whether among the ecological profession or the general public, may ask for everything to be restored completely. Even if actually impossible, to approach such perfection can be immensely difficult. It has lead to planners requiring the transfer, for restoration purposes, of mature forests, which is impracticable. It can lead to immense costs. Certain manipulations, however, such as the retention and replacement of original topsoils, may be the only way to achieve the appropriate endpoint, as in the Australian sand mining industry (Bradshaw and Chadwick 1980). Equally, the total removal of contaminated or highly eutrophic sediments may be the only way to restore the water quality and, therefore, the total ecosystems of some damaged lakes.

But if we are realistic, such major operations may be excessive or impossible in large systems such as the Great Lakes. What is important is to set off succession in the right direction and then leave it to continue itself; this may require preparatory work. Nobody thinks that there is anything wrong in planting small trees to reestablish a forest. But to achieve satisfactory growth it may be necessary to ensure that the soil is fertile or has the means to make it fertile such as by the inclusion of nitrogen-fixing species. This illustrates the importance of ensuring that the functions of the developing ecosystem are properly cared for.

But what are to be the criteria of success? Firstly, should the criteria be based on structure, and in particular the presence or absence of species, or on function, such as plant growth? There is no easy answer, since so much depends on what was the original particular value of the area, and therefore, what is seen to be critical. If the area was rich in wildlife, then the number of species might be the criterion; but if the area was mainly used for agriculture, then crop yield may be the most crucial criterion, as it is in the U.S. Surface Mining Control

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Table 1. A checklist of problems to be found in degraded terrestrial ecosystems, any of which may require treatment, by intervention or natural processes, if restoration is to be successful.

Category	Problem
Physical	
Texture	Coarse, fine
Structure	Compact, loose
Stability	Unstable
Moisture	Wet, dry
Nutrition	
Macronutrients	Nitrogen, others
Micronutrients	Deficient
Toxicity	
pH	Low, high
Heavy metals	High
Salinity	High
Organisms	
Plants	Absent, slow colonization, alien species
Animals	Absent, slow colonization, alien species

Note: A detailed checklist should be made for any habitat requiring restoration.

and Reclamation Act (SMCRA). It could, of course, be some much simpler criterion, such as the amount of heavy metal emanating from a mine site, since water quality down stream will be directly related to this figure.

Secondly, if reliance is being placed on the progressive effects of natural processes, what level has to be achieved? Should 75 or 90% of the preexisting species or plant yield be achieved? There can be no fixed criterion for these, although SMCRA expects 90%. Should metal burdens be reduced to 50, 10, or only 1% of what occurred previously? There are again no easy criteria, although for water there are World Health Organization and individual government standards. For a critical element such as phosphorus in lake water we may from experience take a value such as 100 $\mu g\ P \cdot L^{-1}$ as the critical level in recovery from hypertrophication (Ryding and Rast 1989). But this begs the question as to what is to be considered the original state; is it to be the water quality of 1930, 1950, or perhaps 1500, bearing in mind that human beings have long been part of the ecosystem? In a recent analysis of English lakes, Johnes et al. (1994) suggest the middle 1930s because this is after the full establishment of agriculture but before the advent of intensive agriculture.

Thirdly, once targets have been set, by when should they be achieved? Five years is taken as the period for bond release under SMCRA. But for many natural terrestrial processes such as the accumulation of soil nitrogen, it is not long enough. It can also not be long enough to judge whether interventions are adequate, such as the supply of phosphorus in face of soil phosphorus-fixing processes (Daniels and Zipper 1988). There is no easy answer, except that 3 years is certainly not long enough in either aquatic or terrestrial systems over which to judge success, particularly if restoration has involved major work. What has been done may well last for a few years and then collapse. It was, for instance, not possible to understand the changes taking place in the water quality of the Norfolk Broads, and how they could be combated, in less than a 10-yr study period (Moss 1989). It has taken a similar period of time to establish that a minimum of 1000 $kg\ N \cdot ha^{-1}$ is required for the restoration of temperate terrestrial ecosystems (Marrs et al. 1982).

It is certainly easier to require the presence or absence of particular species by a certain number of years. This does not need detailed understanding of functions and it is easy to specify. Yet this approach is fraught with dangers, especially if species have been artificially reintroduced. They may persist for a few years and then disappear because the restoration of underlying functions has not been addressed properly.

What is crucial is that the development of the ecosystem should be on an upward path in terms of structure and function (Fig. 1), and that no barriers to its long term further development can be envisaged. It is invaluable to have the potential limiting factors in the form of a check list, for example Table 1. This means that both the environment and the process of ecosystem development must be understood. We must also beware of taking any character as a surrogate for the whole development process. In salt marsh restoration for instance, despite its widespread use, the criterion of increased tidal flushing can be misleading, because of complexities in hydrology (Zedler 1988). Should we really put so much stress on biodiversity?

Restoration as an acid test of our understanding

This brings us to the final point, that there is a close relationship between ecological understanding and successful restoration. Indeed, restoration is an acid test of our ecological understanding (Bradshaw 1987*b*), because if we do not understand the processes at work in an ecosystem we are unlikely to be to able to reconstruct it so that it works.

But the relationship is reciprocal, since any attempt to reconstruct an ecosystem is a test of our knowledge of the ecosystem and will reveal any deficiencies in our theoretical knowledge. It is easy enough to take an ecosystem to bits and think that all the significant attributes have been identified. It is only when attempts are made to put it together again that it can be seen whether the bits have been identified correctly. We can learn from our failures.

There is, however, one problem. When restoration is apparently taking place because of the efforts expended, there is the possibility that it could actually be due to the self-restoring properties of the ecosystem, the processes involved in primary succession that we have already discussed. This confusion can be overcome by careful experiments, in which the effects of intervention are compared with suitable controls where there is no intervention.

This raises the role of experimentation in restoration. Such tests cannot be applied unless proper experiments are set up in which critical comparisons can be made. Comparison is an essential aspect of scientific ecology (Bradshaw 1987*c*). The efficacy of different forms of intervention can similarly only be examined in proper experiments, with good statistical design. It should be an essential part of every restoration programme that experimental testing of different aspects of the intervention are carried out. In terrestrial ecosystems this sort of experimentation is easy (Bradshaw and Chadwick 1980). In aquatic systems it is more difficult but equally necessary.

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Finally, it is essential that results are published in journals or reports that are readily available to everyone working in the field. Reviews, including failures as well as successes, are particularly important. It is only by exchange of information that science progresses and that new findings and ideas can be promulgated and developed. Not only should we not have to reinvent the wheel, but also there are generalizations to be made that will allow us to make predictions to guide future action. The development of the science of restoration should go hand in hand with achievements of successful restoration itself.

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Historical causes of change in Great Lakes fish stocks and the implications for ecosystem rehabilitation

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Abstract: To help provide an historical context for habitat modification in support of Great Lakes fisheries, we reviewed changes to Great Lakes commercial fish harvests over the period of 1879–1990 and tabulated the causes associated in the scientific literature with these changes. We also examined the goals promulgated in present fisheries and habitat remediation initiatives that operate locally and lakewide. Changes in the species composition of the harvest are symptomatic of systemic disintegration of native fish communities, perhaps with some indication of recovery in recent years. Of the stresses imposed on the Great Lakes ecosystem, habitat disruption and eutrophication appear to have consistently decreased in intensity and scale. Reevaluation of goals at local and lakewide scales is appropriate because of different scales of management action and because differing responses by species and communities are not adequately recognized. Proposed scales of habitat enhancement are unlikely to produce significant changes to community or ecosystem function, but could affect small and non-diadromous fishes or localized populations such as walleye (*Stizostedion vitreum*) or lake sturgeon (*Acipenser fulvescens*).

Résumé : Afin de dessiner un contexte historique pour les modifications de l'habitat concernant les pêches des Grands Lacs, nous avons examiné les changements survenus dans les prises commerciales de 1879 à 1990 et mis en regard les causes associées à ces changements dans la littérature scientifique. Nous avons examiné, à l'échelle locale et à celle du lac, les objectifs définis pour les pêches actuelles et les initiatives d'assainissement de l'habitat. Les changements observés dans la composition spécifique des prises sont signes de la désintégration systémique des communautés de poissons indigènes, mais sont parfois accompagnés d'indications de rétablissement depuis quelques années. Parmi les stress subis par l'écosystème des Grands Lacs, on note deux cas, soit la perturbation de l'habitat et l'eutrophisation, pour lesquels on a observé ce qui semble être une diminution constante d'intensité et d'échelle. La réévaluation des objectifs à l'échelle locale et à celle du lac est pertinente à cause des diverses échelles des activités de gestion et parce que les différentes réponses des espèces et des communauts ne sont pas adéquatement reconnues. Les échelles proposées des mesures d'amélioration de l'habitat n'occasionneront vraisemblablement pas de changements significatifs au niveau des fonctions communautaires ou écosystémiques, mais elles pourraient toucher les poissons de petite taille ou non diadromes, ou les populations localisées comme celles de doré *(Stizostedion vitreum)* ou d'esturgeon jaune *(Acipenser fulvescens)*.
[Traduit par la Rédaction]

Introduction

Habitat modification, eutrophication, exploitation, introduction of exotic species, and contaminants have been variously invoked as stressors affecting the status and well-being of fish stocks in the Great Lakes (see the SCOL 1972, PERCIS 1977, and ASPY 1987 symposia published in the *Canadian Journal of Fisheries and Aquatic Sciences* for examples). This identification and treatment of stressors in ecology (Esch and Hazen 1978; Odum 1985) has undergone considerable evolution and has been incorporated into a science and policy framework (Odum 1963; IJC 1970; Edwards and Regier 1990) to develop binational agreements and efforts intended to rehabilitate and restore Great Lakes ecosystems.

Initiatives to rehabilitate or restore ecosystem integrity in the Great Lakes target both remediation of severely degraded localized areas (e.g., IJC Areas of Concern (AOCs)) and resource management at the whole system level (e.g., Ontario Ministry of Natural Resources (OMNR) Lake Management Plans and the Strategic Plan for Management of Great Lakes Fisheries developed through the Great Lakes Fishery Commission). Rehabilitation and restoration efforts at these different scales may be complementary, as the underlying stressors may act at different scales. For example, spawning areas are localized, but their disruption could affect discrete fish stocks, and sources of nutrients can eutrophy local embayments, e.g., Batchawana Bay in Lake Superior, or whole lake basins e.g., Lake Erie.

Scientific interpretations and management decisions relating to both local- and ecosystem-scale management are complicated by our failure to fully explore historical records, including those related to fisheries. Historical analysis can provide insight into interrelations between the spatial scale and

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temporal dynamics of the stressors and the response of the fishery or the entire ecosystem (e.g., Steedman et al. 1996). For example, historical evidence from the Great Lakes region frequently suggests the occurrence of interacting and simultaneous stressors, non-diagnostic symptoms, and delays between cause and effect in the interactions of human activity and aquatic ecosystems. Some ecological symptoms that management agencies are addressing today may be a complex response to a long-term and complicated sequence of stressors, some of which may no longer be active or important.

Ryder and Kerr (1989) stressed the need to develop prior knowledge of the major environmental determinants before introduction of management initiatives, including habitat modification. The scale of the Great Lakes introduces opportunity for "noise" to contribute a masking effect upon those ecosystem properties, and their changes, that affect ecosystem performance. The effects of some human activities can meld with or mask natural processes affecting early life survival and subsequent recruitment of fish stocks. This has been noted for both hydrocarbon exploration (Ware 1982), and for once-through cooling of electrical generating stations (Kelso and Milburn 1979). These inherent problems in relating cause to effect, however, do not obviate the need to identify distinctive properties of change at large system scales, and to use the historic lesson to direct fledgling ecosystem-based management initiatives.

To provide an historical context for habitat modification strategies designed to benefit fisheries and achieve ecosystem rehabilitation goals, we reviewed fishery and aquatic ecosystem responses to human activity in the Great Lakes basin, analyzed evidence for "cause and effect" associations in an historical context and evaluated the significance of habitat conservation and restoration as an element of Great Lakes management.

Great Lakes ecosystem responses to human uses and abuses

Ecosystems are open systems that continuously exchange material and energy with their environment. While ecosystems may evolve in the long term toward increasing complexity and functional capability (see review in Steedman and Regier 1987, for example), change and "resets" are ubiquitous and normal in many environments (Lane 1986) and may arise as a result of external environmental stresses or complex internal processes.

It may be possible to unequivocally relate the effect of a change in a single factor (e.g., temperature) on the well-being of a single fish (Fry 1947; Kerr and Lawrie 1976), but it is another matter to interpret the complex responses of multispecies fish community to a suite of stressors such as those associated with urban-industrial development of a lake catchment. The response of such a fish community may be gradual over some range of stress, but may be dramatic, discontinuous, or catastrophic over another range of the same stress. In addition, the response to remediation of stress may not be a simple reversal of changes that occurred as the stress was building, i.e., "hysteresis" can occur (Steedman and Regier 1987). This complexity of biotic response to stress (and by extrapolation, response to stress removal or reduction) is exemplified by the fertilization experiment in Great Central Lake, British Columbia (Barraclough and Robinson 1972; Robinson and Barraclough 1978). It was hypothesized that fertilization would increase primary production and enhance the production of juvenile sockeye salmon (*Onchrohynchus nerka*). The net effect from fertilization was that production of the juvenile salmon that utilize the pelagic waters of the lake as a nursery area was enhanced through increased survival rather than enhanced growth or a greater average weight of emigrants.

Certain generalities of ecosystem response to stress have been widely observed (Regier and Cowell 1972; Margalef 1975; Odum 1985; Rapport et al. 1985) but are difficult to quantify. The following qualitative symptoms of systemic disintegration or reorganization of fish communities in response to complex human intervention have been recognized in Great Lakes ecosystems (Steedman and Regier 1990): (*i*) A shift in dominance from large, long-lived (lake trout (*Salvelinus namaycush*), lake sturgeon (*Acipenser fulvescens*)) to small, short-lived fish (alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*)); (*ii*) A shift from populations where abundance and age are relatively constant to populations that fluctuate in the short term, e.g., lake herring (*Coregonus artedii*); (*iii*) A shift from communities that are associated with diversity in morphometry (shorelines, shoals, and physical structure) to those that thrive in less-structured open-water environments (e.g., decreased reliance of fisheries on walleye (*Stizostedion vitreum*), lake sturgeon, and black basses and increased reliance on herring, lake whitefish (*Coregonus clupeaformis*), and smelt); (*iv*) A shift in abundance from species preferred by humans for food or sport (e.g., lake trout, whitefish, salmon) to those that are not (e.g., smelt, alewife, suckers).

These responses by the endemic, self-sustaining Great Lakes fish community may have been affected by recent (post-1960) stocking of lake trout and Pacific salmon to provide sport fishing opportunities, particularly in Lakes Michigan and Ontario. Additional complications have probably resulted from introductions of exotic species (Mills et al. 1993), some affecting trophodynamics (e.g., zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*)) and others occupying important nearshore niches (e.g., ruffe (*Gymnocephalus cernuus*)).

Interestingly, recent increases in lake trout and walleye, and decreases in smelt abundance in Lake Ontario (Christie et al. 1987) seem to indicate reversal of several of the stress responses identified above. It may be that 40 years of restoration and rehabilitation efforts directed to sea lamprey (*Petromyzon marinus*) control, lake trout stocking, and fish population management are now providing obvious benefits in Lake Ontario.

Factors contributing to changes in Great Lakes fish communities

In the Great Lakes, many significant or destructive effects of human activity may be behind us (Fig. 1). According to Beeton's (1969) synthesis of human population information from the early 19th century in the Great Lakes, the earliest decade of rapid population expansion (approximate tripling) was that of the 1820s in the Lake Ontario basin, the 1840s in Lake Erie, the 1860s in Lakes Michigan and Huron, and the 1900s in Lake Superior. Whole-lake chemical change was subtle and gradual following these years of population expansion and

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Fig. 1. Relative magnitude and approximate time frame of some stressors operating upon the Great Lakes ecosystem. Data are from Baldwin et al. (1979), Beeton (1969), Hermanson et.al. (1991), International Joint Commission (1994), Kelso and Minns (1979), Mills et al. (1993), Ministry of Northern Development (unpublished data), Ministry of Northern Development and Mines (unpublished data), Ontario Department of Lands and Forests (1959, 1968), Ontario Ministry of Natural Resources (1977, 1982, 1986, 1990), Reed (1991), Statistics Canada (1989, 1993), and U.S. Army Corps of Engineers (1957, 1977, 1978–1992).

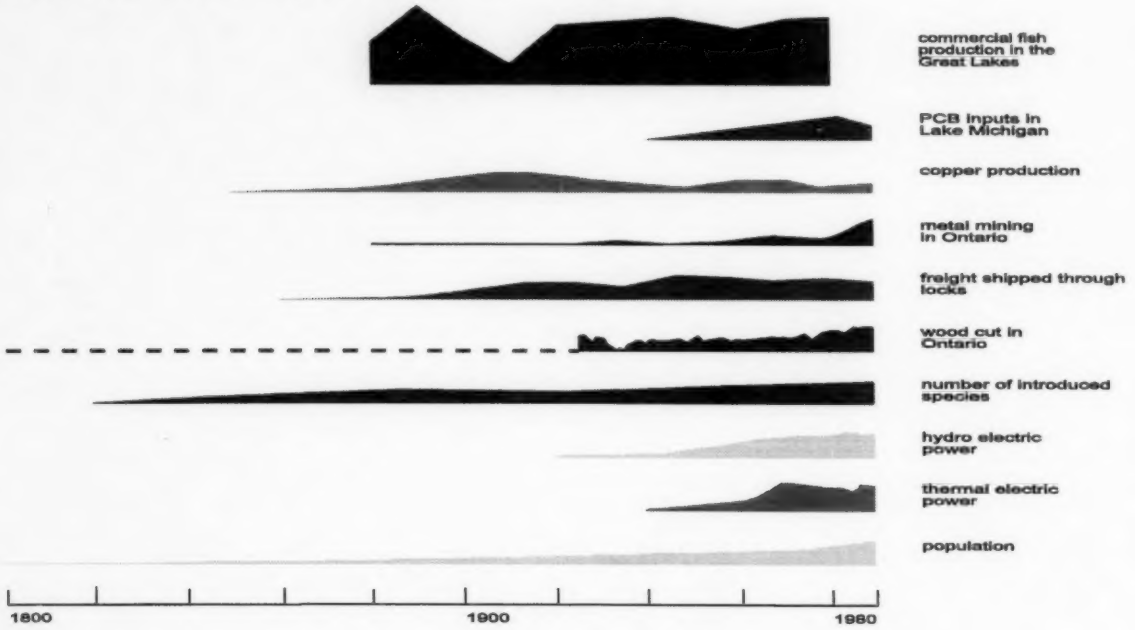
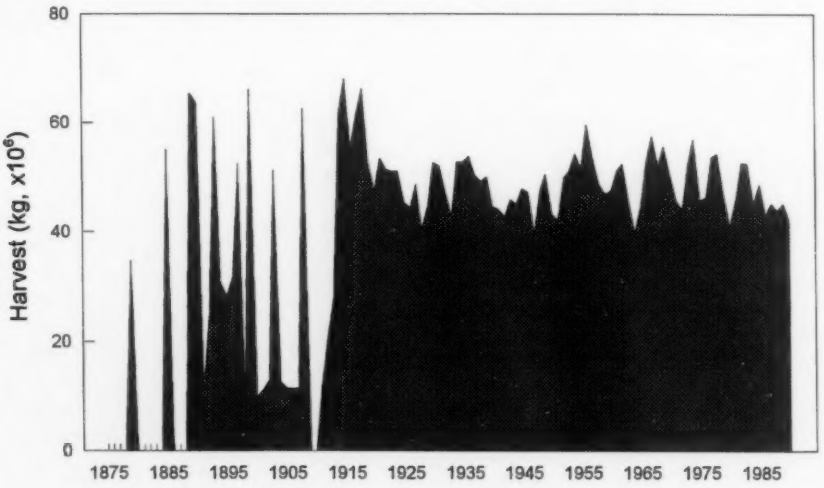


Fig. 2. Commercial fish harvest, all species and jurisdictions combined, for the Great Lakes 1879 to 1990.



increases in nutrient or trophic related chemistry were detectable in Lakes Ontario, Erie, and Michigan. In Lake Huron, whole-lake change in chemistry was apparent several decades after early population expansion; chemical change is still not apparent in Lake Superior (Beeton 1969). Excessive exploitation depleted fish stocks even in the mid-1800s (Smiley 1882). Gross alterations to watersheds had curtailed spawning runs of whitefish in Lake Michigan by the mid-1800s and Atlantic salmon (*Salmo salar*) were being affected by dams, sawdust from lumber mills, and pollution from industries such as tanneries from about 1840 onward (Goode, in Danfield 1985).

Unfortunately, early documentation of habitat disruption is

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sparse or has not been summarized from diffuse and obscure sources. We are left to infer changes from early growth in human population and industry (Fig. 1). However, it is certain that pervasive effects from catchment deforestation associated with the pineries and early agricultural land clearing lasted throughout the 1800s. Stream channelization, removal of "obstacles" from streams, damming, and organic pollution related to water transport of wood lasted until 1972 when the last log drive occurred in the Great Lakes basin (Kelso and Demers 1993).

Certainly the days of rapid population increase, settlement, eutrophication, and industrial growth appear constrained today in the Great Lakes. In Ontario, the 1980s and 1990s have seen economic recession, relatively stable urban populations, and declining rural populations. These phenomena, along with increasing environmental awareness in citizens of the Great Lakes region, have resulted in improved water quality and lowered productivity in Lakes Erie, Ontario, and Michigan (e.g., Wolin et al. 1991). There is also evidence that concentrations of toxic persistent chemicals have declined (e.g., Hermanson et al. 1991; Borgmann and Whittle 1992; Suns et al. 1993).

We do not suggest that watershed alterations caused by more recent processes such as aerial and point-source inputs of persistent toxins, continued introductions of exotic species, and persistent effects from damming or modifying streams are not of significant concern. However, pollution from watershed land use activities has declined in areas and resulted in nutrient reductions; new harbour development and channelization for commercial shipping is decreasing because fewer goods are transported by water, no hydroelectric generating stations 20 MW have been constructed since the 1960s (A.E. Christie, Ontario Hydro, Toronto, Ont., personal communication) and, while logging activities continue in the Great Lakes watershed, log drives have ceased.

Analysis of fish community trends

Reported annual commercial fish harvest in the Great Lakes has remained near 45 000 t throughout most of this century (Fig. 2), but changes in species composition of the harvest are symptomatic of systemic disintegration of native fish communities, perhaps with some recovery in recent years. Changes in the Great Lakes fish community can be treated as an ecological time series (Legendre and Legendre 1983) and have been analyzed repeatedly for at least the last century (see Smith and Snell 1891; Nute 1926 as early examples). The commercial fish harvest data base spans the longest period of any ecological data base in the Great Lakes (Fig.2). These data have been intensively mined particularly to identify changes in the commercial harvest and to form a basis upon which to infer cause for the observed changes. While the data for the Great Lakes have been used by many, differences in their interpretation arise. For example, Cleland (1982) stated that the peak of commercial fish production for Lakes Huron, Michigan, and Superior occurred in 1885, earlier than suggested by Berst and Spangler (1972), Wells and McLain (1972), and Lawrie and Rahrer (1972).

We chose not to resolve conflicts or reexamine the data base, but to enumerate from the available literature all reference to change in abundance for any species. With each mention of change in abundance in key citations (see Fig. 3 legend) we noted whether the change was an apparent increase or decrease, the decade when the change became apparent (if an increase, for example, began in the 1920s and continued through the 1940s, we assumed events in the 1920s were important) and the cause attributed to the change.

Causes of fish community change

We then classified published evidence for change in fish communities into four groups, according to the underlying cause identified by the author(s) of each paper: factors related to abundance (exploitation, stocking, fish population management); effects from exotic species (introductions, changes in their abundance); effects from habitat change; and endemic or natural processes (disease, biotic interactions, climate). We organized the identified causes by decade and expressed the causes of change for each lake in relation to the number of species for which a change was cited throughout the time period. The time series that this analysis was based on is biased toward identifiable causes producing an obvious change in harvest, species for which change was readily apparent, and situations (local or lakewide) for which data were available. However, this treatment reduces the reliance on a single or most recent citation and cumulates, perhaps, an evolving consensus.

We were unable to construct a complete time series (Fig. 1) of the factors that might contribute to change in the fish community. Of the trends that we were able to document, it seems that the late 1800s, the 1920s and 1930s, and the 1950s and 1960s were periods of human population increase that brought new exotic species, increases in economic activity (reflected by two-way shipping through the locks of Sault Ste. Marie), and increased ore production. Increasing wood production and thermal and hydroelectric power generation might have been expected to continue the early trends of habitat modification begun by harbour construction and waterway modification (primarily for transport of wood) but were not invoked as possible causes effecting change in the fish community. As well, continuing invasions of exotic species do not appear to be contributing to declines in the commercially harvested fish species at least until the 1980s.

It appears the Great Lakes fish community collectively (Fig. 3) underwent noticeable change in the late 1800s, the 1920s–1930s, and in the 1950s–1960s. These changes were apparent in Lakes Ontario, Huron, Michigan, and Superior. On average, more fish species appeared to increase than decrease in abundance in the 1870s, 1900s, 1930s, and from the 1960s to the present. The three periods of greatest change in fish abundance in the Great Lakes are comprised of both gains and losses. The tendency toward greater change (or perhaps a greater awareness of change) increased over the period of record.

The relationship between changes in fish populations and the four classes of cause were examined in 40-year time steps, from 1870 to the present (Fig. 3). Introductions and stocking of exotic fish species, and endemic processes such as favourable reproductive conditions, were cited as contributing to increases in abundance of Great Lakes fish populations. Conversely, perturbed habitat, exploitation, and introduction of exotic species were cited as contributing to decreased abundance. Exploitation and stocking, contributing to either increases or decreases in the abundance of the fish harvest, have

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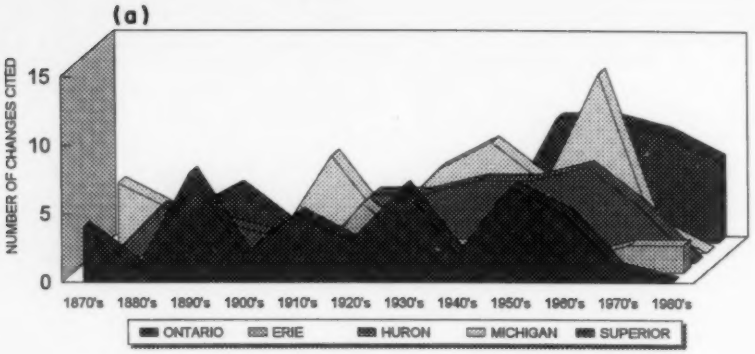

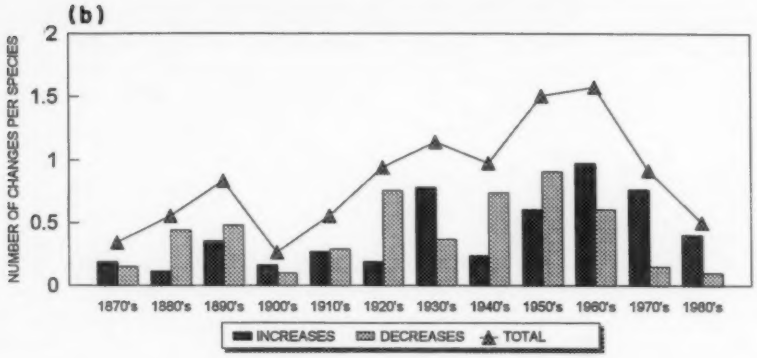

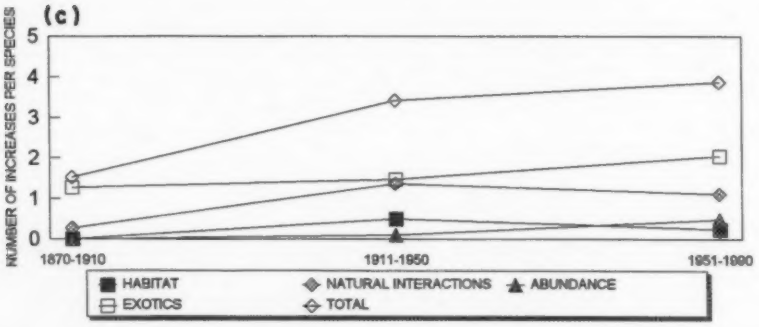

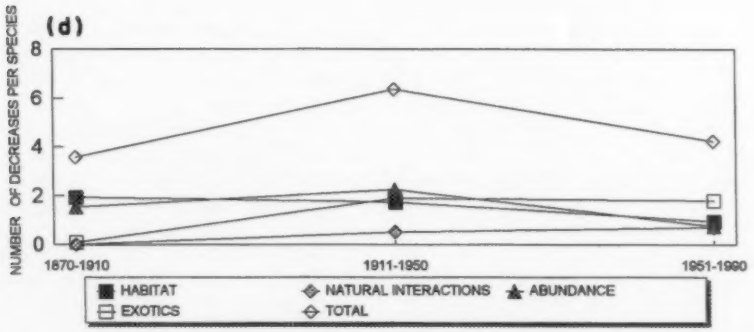

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Fig. 3. Number of cited changes (A), decade of change (B), increase (C) or decrease (D) and class of perturbation attributed to observed changes in Great Lakes fish populations (see text). Data are from Beeton (1969), Berst and Spangler (1972), Christie (1972, 1973, 1974), Collins (1988), Desjardine et al. (1995), Eck and Wells (1987), Evans (1988), Habitat Advisory Board (1993), Hansen (1990), Hartman (1972), Lawrie (1978), Lawrie and Rahrer (1972), MacCallum and Selgeby (1987), Moffet (1957), Rathke and McRae (1987), Regier and Hartman (1973), Schneider and Leach (1977), Sly (no date), Smith (1968), Smith (1970), Spangler et al. (1977), VanOosten (1930), and Wells and McLain (1972, 1973).

acted over the period of record. Most factors assumed to contribute to change in the fish community varied over time.

Of the four classes of "cause", only habitat disruption appeared to decline in intensity and scale since the early 1900s. We infer that its effect upon the commercial fishery and the extant fish community has also decreased. There is an association between habitat destruction and the declining commercial fishery prior to the 1920s; later, no relation is apparent from citations in the literature. Pre-1920 habitat disruption included removal of boulders, rapids, and "obstructions" to river log drives; along-shore construction of road beds for transport; flow control structures; and alteration of, particularly, embayments and estuaries to accommodate ports and towns.

A number of factors may contribute to the perceptions derived from an integration of cause and effect from the literature. First, the early commercial fishery was primarily dependent or focused on lake trout, whitefish, sturgeon, walleye, and herring; changes in these species were of primary concern and their abundance was closely followed. Recently, the focus has broadened to include other species in the fish community; thus, recent interpretation of change or trends may be from both a community and a species perspective. Second, changes in the fish community may take unexpectedly long periods before becoming obvious, and the passage of time may obscure the linkage between cause and effect. Third, the response to increasing or decreasing stress may not be direct or linear. Fourth, merging results and interpretations from the literature may obscure the appropriate deduction. Finally, the complex history of increasing and decreasing stressors may have disrupted Great Lakes fish communities to the extent that wide fluctuations in fish abundance are now a permanent fixture of the ecosystem.

Aquatic habitat as a manageable element of Great Lakes ecosystems

Management initiatives to restore Great Lakes fish communities often involve an element of habitat restoration. It is important to understand the cause of habitat degradation, since this will affect the techniques used to restore lost habitat features. Successful habitat restoration also requires an understanding of the scale at which the ecosystem or community in question has been affected by habitat degradation. These types of understanding have been impaired by the lack of a clear definition of the word "habitat."

The term habitat has come to denote far more than the "natural home of a plant or animal" as defined in the Concise Oxford Dictionary (1974). In its broadest sense, habitat is used to refer to "the space in which biota live" (Sly and Busch 1992). Definitions vary from text to text (e.g., Clarke 1965; Odum 1971; Krebs 1978; Smith 1980), and consensus among ecologists appears to extend only to the fact that biota live in and use habitat. Attempts have been made to classify habitat at a variety of scales and resolutions. However, disagreement on definitions of habitat types or classes and their role in ecosystem production processes remains (Hammer 1991).

Scientists and natural resource managers use the word habitat to refer to a variety of small-scale physical and structural features of ecosystems believed to be important to animals in aquatic environments. Each feature is associated with a life activity or requirement, e.g., spawning habitat, nursery habitat, refuge. At this scale, it may be effective to use engineering or "landscaping" techniques, manipulating the physical features of the area, to restore habitat.

The meaning of habitat at an extensive, ecosystem-level scale is more nebulous. At this level, "good habitat" has become analogous with system integrity, referring to healthy, self-organizing natural systems that support a variety of species. An example of such a large-scale habitat degradation would be nutrient eutrophication or inputs of toxins. Large-scale restoration may be possible by reducing or removing the inputs.

Stress reduction should be implemented and evaluated at scales appropriate to the perturbation (e.g., square metres of spawning habitat created, hectares of wetlands restored, contaminant load reduction related to watershed areal units). Regardless of the type of remediation, the effectiveness of rehabilitation efforts should be gauged by the response of the ecosystem. Only if the ecosystem responds favourably to a reversal, reduction, or removal of the cause of habitat degradation can habitat restoration by judged as successful.

Confusion (or profusion) of goals

Remedial Action Plans (RAPs) developed for Great Lakes AOCs, and lakewide fishery management plans developed under the auspices of the Great Lakes Fishery Commission both target environmental, fish species, and biotic community goals in their efforts to restore the Great Lakes ecosystem (Fig. 4). The management initiatives invoked by these goals, once developed and accepted, will be at different scales ranging from local to lakewide and may be directed at fish species or fish communities.

Twenty-nine fish species, four families, and several broad groupings of fishes (e.g., forage species) are targeted for management in the above plans. Species or groups of fishes are targeted for reestablishment (where extirpation has occurred, e.g., muskellunge (*Esox masquinongy*), herring, lake sturgeon, brook trout); reduction (only sea lamprey proposed as requiring reduction in abundance); restoration, rehabilitation, and maintenance; and control for white perch (*Morone americana*), carp (*Cyprinus carpio*), and suckers in Lakes Huron, Michigan, and Erie. The distinction between "restore" and "rehabilitate" and "reduce" and "control" was unclear in the statements of management goals. For the purposes of our tabulation, if the stated goal of a plan was to achieve an historical level of commercial production or abundance we used restora-

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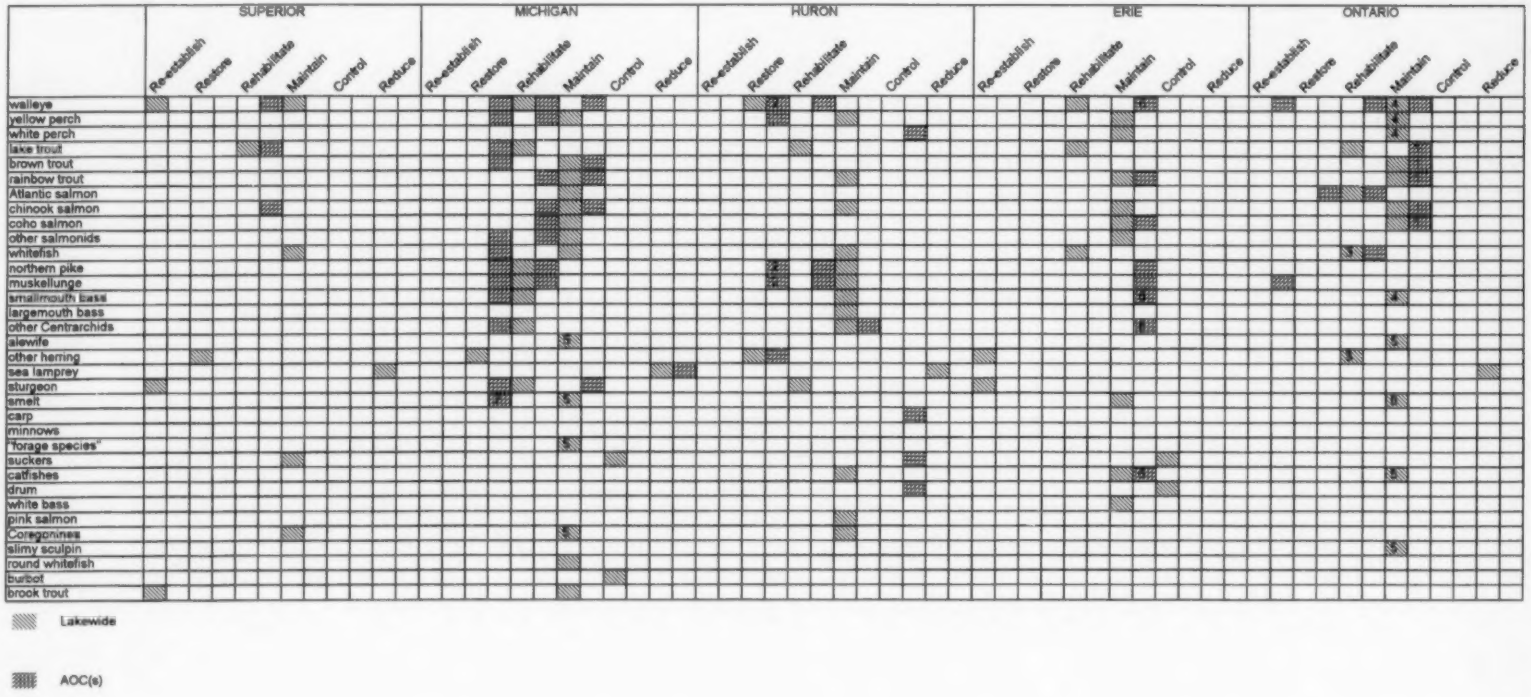
Fig. 4. Fish community objectives in the Great Lakes and Areas of Concern. As examples of the difficulties in categorizing objectives into the above six modes of management, we have included several notes referring to the description of the objective: (1) "protect, restore, and enhance fish stocks" via stocking and "maintain and enhance a diverse mix of sport fish" (2) to 1970s levels; (3) managed to maintain diversity although species are at low levels of abundance (does not say whether an increase is desirable); (4) "maintain as part of a complex at historical levels; (5) managed to achieve a desired annual biomass as part of a complex and not on a per species basis; and (6) managed to support a warmwater fishery.



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tion. We used the term rehabilitation when the stated goal was to reach a level of abundance without an historical reference or precedent. When goals were not mentioned in a clear context, we used the originator's terms.

At different scales within lakes, management initiatives differed in their recommendations for species-specific management action. This inconsistency was most pronounced for management initiatives in Lakes Superior, Erie, and Ontario, relative to Lakes Michigan and Huron. As an example, in Lake Huron, yellow perch were identified as requiring restoration (implying a reduction from historic abundance) lakewide, but were only to be maintained in their abundance at AOCs. We infer either that the species is abundant locally or that, at a smaller scale, another species is more deserving of attention. In Lake Ontario AOCs, 16 species including both warm-and cold-water species and a wide range in lifestyles are targeted. The lakewide program identifies only cold-water species in their goals. Similarities among goals established lakewide and at AOCs do exist but are fewer. Plans may, therefore, be inconsistent.

Generally, lakewide goals set by resource managers seem constrained to species of sport or commercial interest. Salmonines, coregonines, and walleye are consistently identified as requiring restoration throughout the Great Lakes. At AOCs, where the partners come from most sectors in society, a diversity in the biotic community, reflecting to some degree ecosystem integrity, has been identified for restoration and rehabilitation.

Perhaps most inhibiting to management initiatives is the diversity in species identified for restoration and the disagreement in perception of the status of a species (i.e., that a species might require restoration, rehabilitation, or conservation). Management actions will clearly differ if evoked by different perceptions of well-being. It seems unreasonable that management actions within a lake should apply lakewide, with local exceptions. It also seems unreasonable that an environmental remediation program at AOCs would set goals at odds with lakewide fish management action, particularly if environmental or habitat remediation is required to manifest lakewide goals. Therefore, action to produce objectives that are clear and complementary at lakewide and local scales is necessary.

Lessons for rehabilitation

Although reported commercial fish harvest since its inception in the Great Lakes has remained near 45 000, the species and their contribution to that harvest have changed throughout. These changes in the fishery resulted in systemic alteration of the community and produced symptoms of both disintegration and, perhaps, recent positive responses to rehabilitation efforts. Limited consensus exists in the scientific literature as to causative stressors for the changes in Great Lakes fish stocks. However, underlying factors affecting abundance (e.g., exploitation and population management), effects from introduced and invading exotic species, and endemic processes (e.g., disease, climate) consistently have been assumed to be causative factors affecting the fishery during its history.

The rate of habitat change seems to have decreased in intensity and scale since the early 1900s, and we infer that its effect upon the commercial fishery and the extant fish community has also decreased. Unfortunately, because the changes to the physical and chemical characteristics of the Great Lakes have been significant and pervasive, our scope for effective restoration might best be described as "tinkering," or providing only incremental beneficial effects, particularly in the case of habitat restoration. This would suggest that gains in fish community biomass are unlikely to be made by habitat enhancement. Incremental increases in habitat quality and diversity should probably be made to the most perturbed environments to improve local diversity and contribution to community biomass.

Reevaluation of goals to more closely align with realistic expectations are required by RAPs and Great Lakes (GLFC) Technical Committees. For the same lake, these initiatives may differ in their target for the same species. Lake management initiatives are major vehicles for delivery of conservation and protection initiatives; RAPs may lead to incremental improvement to habitat. Appreciation of the scale of management action and alignment of goals and expectations with management action and scale of action also are important to successful Great Lakes remediation.

Managing Great Lakes fish stocks in a changing ecosystem may be akin to managing surprise, at least at the species level (Edwards and Regier 1990). Conversely, commercial fish harvest (Fig. 2) and fish community biomass and production (Kelso and Johnson 1991; Randall et al. 1995) tend toward stability. The consequence of these different operating principles of species and communities should be reflected in both actions and goals. The current scale of habitat enhancement is unlikely to provide substantial gains to community or ecosystem. Localized changes to non-diadromous (small fishes) or local populations (walleye, lake sturgeon) are likely to be larger.

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A model simulating the impact of habitat supply limits on northern pike, *Esox lucius*, in Hamilton Harbour, Lake Ontario

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Abstract: The effects of life-stage habitat supply limits on fish populations are examined using a simple model of northern pike (*Esox lucius*). The model has submodels for spawning, fry, and juveniles + adults (1+). The modelling approach assumes the habitat supply for life stages can be estimated and the key population processes in each life stage are controlled by a saturation function of habitat supply. Only one life stage can limit the population at a time. Baseline simulations show that fry and juvenile–adult habitat supplies are more limiting than spawning habitat, contrary to conventional wisdom. Paradoxically, spawning habitat may be rarer in absolute terms but other life stages need more of the total lake ecosystem area to be suitable for the population to succeed. Simulations based on a simple depth-based model of suitable habitat show how lake depth and hypsographic shape can affect population size and structure. Population sizes generated with various habitat supply scenarios overlap the reported range of values. The application to Hamilton Harbour shows how a dynamic model with habitat supply limitations can guide restoration efforts. Habitat management and conservation assessments must consider the dynamic population responses to varying life-stage habitat supplies.

Résumé : Afin de déterminer dans quelle mesure les populations de poissons sont limitées par la disponibilité des habitats convenant à chaque stade du cycle vital, nous avons appliqué au grand brochet un modèle simple comprenant des sous-modèles pour les stades de la fraye, des alevins et des poissons jeunes et adultes (1+). Nous avons pris pour acquis qu'il est possible d'estimer la disponibilité des habitats et que les principaux processus démographiques caractérisant chaque stade sont contrôlés par une fonction de saturation de la disponibilité des habitats. Un seul stade à la fois peut limiter la population. Les simulations de départ ont montré que la disponibilité des habitats de fraye et la disponibilité des habitats des jeunes et des adultes ont un effet limitant plus prononcé que la disponibilité des habitats des alevins, contrairement à ce qu'on croit généralement. Paradoxalement, les habitats de fraye peuvent être les plus rares en quantité absolue. Cependant, dans le cas des autres stades, il faut qu'une portion plus grande de la superficie totale de l'écosystème du lac soit utilisable pour que la population se maintienne. Des simulations réalisées selon un modèle simple, décrivant la qualité des habitats en fonction de la profondeur, montrent que la profondeur et le profil hypsographique du lac peuvent influer sur la taille et la structure de la population. Les tailles de population obtenues selon les divers scénarios de disponibilité des habitats recoupent les gammes de valeurs déjà signalées. L'application de la méthode au havre de Hamilton montre qu'un modèle dynamique tenant compte de la disponibilité des habitats peut servir de guide pour les mesures de restauration. Les évaluations réalisées aux fins de gestion et de conservation des habitats doivent prendre en considération la réaction des populations aux variations de la disponibilité des habitats de chaque stade.
[Traduit par la Rédaction]

Introduction

Most extinctions of freshwater fish have been caused by habitat alteration and destruction (50%), followed by exotic species introductions (37%) and overexploitation by humans (8%) (Thomas 1994). Human activities have disturbed or dominate 48% of the earth's land area (Hannah et al. 1994). Wherever humans disturb the land, they also alter the freshwaters. In Canada, more than 40 freshwater fish species, out of a total of ≈200, are listed as vulnerable, threatened, or endangered (Campbell 1993). Despite best intentions, humans are continuing to encroach on the habitats needed to support freshwater fish and fisheries. Successful conservation of healthy, diverse, self-sustaining fish resources and sustainable fisheries requires that habitats be protected and that exploitation rates be limited to safe levels. Habitat is the essential foundation upon which fish populations thrive and fisheries prosper.

Studies of fish populations often appear to be evolving along two distinct paths, one centred on the dynamics of populations in relation to their exploitation and another focused on the static relationships between fish and their habitats. Dynamic numerical models of fish populations have often been used to examine the interaction of population processes, such as growth, mortality, and recruitment, with abundance and to identify exploitation limits (Beverton and Holt 1957; Ricker 1958, 1975). Such models are usually site specific with no explicit effort to quantify the effects of habitat supply limits that must always, by some means, control the size and dynam-

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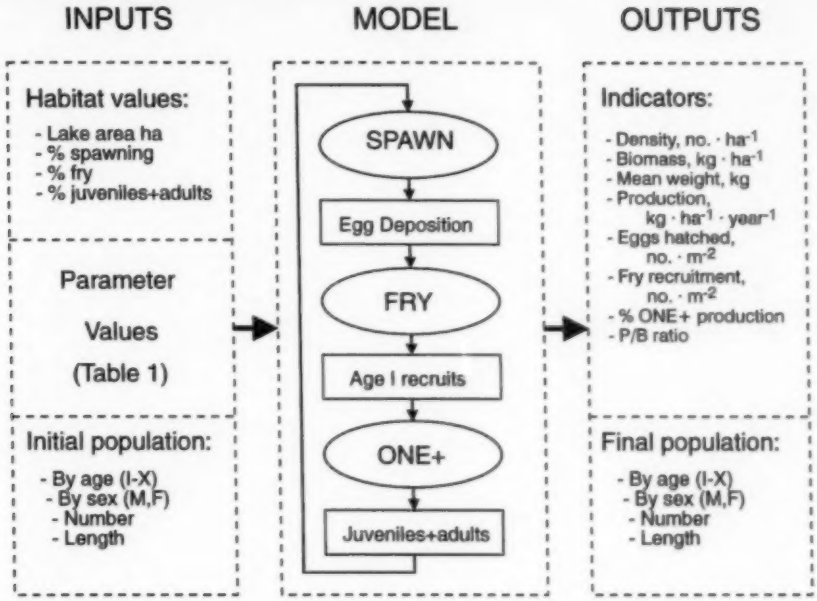
Fig. 1. Schematic of the northern pike population–habitat modelling framework.



ics of fish populations. Modelling is also an increasingly important component of efforts to assess the significance of habitat in fish population dynamics (Tyler and Rose 1994).

Few frameworks for assessing the impact of habitat supply limits have been proposed. In the United States, the Fish and Wildlife Service developed the Habitat Evaluation Procedures (HEP) for fish and wildlife resources, which epitomize a static approach to fish–habitat relationships based on habitat suitability index (HSI) models (USFWS 1981; Terrell et al. 1982). HSI models assume that (*i*) the abundance of fish, or wildlife, is linearly related to the supply of suitable habitat and (*ii*) the relative suitability of different habitat areas can be measured by a proportional index. Minns et al. (1993*a*, 1993*b*) derived a similar approach to habitat evaluation based on the Ultimate Environmental Threshold (UET) ecosystem planning method of Kozlowski (1985, 1986). The UET approach focuses on the productivity of habitats and integrates the impact of both habitat loss, by including a uniqueness factor, and habitat deterioration due to load-driven, nondestructive stresses such as eutrophication and acidification.

Both HEP and UET schemes arrive at overall suitability values by aggregating estimates of suitability of different habitat features for various life stages of the target organism. These approaches take no account of the potential interactions among different life stages subject to different habitat supply limits.

In this study, the first objective was to construct and evaluate an age-structured fish population model that explicitly relates density-dependent effects in various life stages to the supply of habitat suitable to each life stage. The species selected for this study was northern pike (*Esox lucius*). The second objective was to use the resulting model to predict pike population size and composition under a range of habitat scenarios in Hamilton Harbour, a degraded ecosystem on Lake Ontario.

Model development and rationale

The modelling framework has three components: inputs, model, and outputs (Fig. 1).

Inputs

The input section has three components: (*i*) specification of habitat supplies, (*ii*) model parameters, and (*iii*) a founding population structured by age and sex. The habitat inputs are (*i*) the total ecosystem or lake area (hectares) and (*ii*) the proportions of that total area assumed to represent weighted usable areas (WUAs) for spawning, fry, and juveniles + adults (1+), the three life stages represented in the model. Each set of these habitat measures is a scenario that interacts with the model. The parameter values are those used in the model equations described in the following sections (Table 1). Parameter values translate the concepts embodied in the model equations into numerical prediction and introduce a fixed relational scaling of all elements of the model. The initial population consists of the total number and fish length, in millimetres, of each sex in each age-class, 1–10. The derivation of the initial population structure is described below. The initial population establishes the population in the model at time $t = 0$ years, predicting the population at $t = 1$. After that, the population at time $t = i$ is used to predict the population at $t = i + 1$.

Model

The simulation model was developed using the explicit assumption that weighted areas of usable, or suitable, habitat (WUAs), derived from HSI or UET evaluation models, provided an estimate of the habitat supply specific to each life stage. The model was also developed with the expectation that it would be applicable to different lakes if the total area and proportional life-stage habitat supplies could be estimated. Data on pike life history compiled by Raat (1988) was the primary source of information used to build the model's equations. Crossman and Casselman's (1987) extensive literature review on pike was also helpful.

Based on identified pike habitat requirements (Inskip 1982; Minns et al. 1990, 1993*b*), the population model divides into three components, each with discrete habitat area requirements: (*i*) SPAWN,

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Table 1. Listing of parameters and the values selected for the northern pike population–habitat simulation model.

	Life stage or sex			
	Fry	Male	Female	Equation
L (mm) – W (g) equation constant	—	0.000004	0.000004	1
L (mm) – W (g) equation exponent	—	3.059	3.059	1
Eggs – L (cm) equation constant	—	—	0.000006	2
Eggs – L (cm) equation exponent	—	—	3.527	2
Minimum L (mm) at maturity	—	300	350	
Maximum L (mm) at maturity	—	450	500	
Min. spawning L multiplier, M_{SMIN}	—	1	1	3
Max. spawning L multiplier, M_{SMAX}	—	80	80	3
Proportion of successful eggs when $AS_{ACT} = AS_{MAX}$	—	0.99	0.99	4
Proportion of successful eggs when $AS_{ACT} = AS_{MIN}$	—	0.01	0.01	4
Max. fry survival rate, fa	7.65	—	—	9
Max. decrease in fry survival rate, fb	31.73	—	—	9
Constant in saturation equation, fd	41.70	—	—	9
Exponent in saturation equation, fc	0.31	—	—	9
L (mm) of newborn fry	7.25	—	—	
L (mm) – W (g) equation exponent for fry	1.75	—	—	
L (mm) – W (g) equation constant for fry	0.000192	—	—	
Population area/individual equation constant	—	0.000031	0.000031	13
Population area/individual equation exponent	—	2.59	2.59	13
Home range equation constant	—	2.74	2.74	12
Home range equation exponent	—	1.52	1.52	12
Annual juvenile+adult survival rates	—	0.45	0.65	
Max. L (mm) at age 1	—	280	280	
Max. L (mm) at age ∞	—	950	1100	11
Proportion of max. growth when $AA_{ACT} = AA_{HR}$	—	0.99	0.99	14
Proportion of max. growth when $AA_{ACT} = AA_{POP}$	—	0.50	0.50	14

covering the period from spawning through to egg hatching; (*ii*) FRY, from hatched eggs through to recruitment at age one; and (*iii*) ONE+, all juvenile and adult year-classes. An annual cycle is followed with life-stage events occurring in sequence. Spawning and egg hatching occur in the spring. Young-of-the-year (YOY) growth and survival are computed through to age 1 for the next spring. Juvenile + adult growth and mortalities (natural only but fishing could be added) occur. In the following spring, juveniles and adults age by 1 year and the surviving YOYs from the previous summer become the age 1 class. All modelling elements involving body size use fish length. Fish weights, which were needed to calculate biomass and production, were computed using a standardized length (L; millimetres) – weight (W; grams) relationship (Willis 1989):

$$(1) \quad \log_{10} W = -5.369 + 3.059(\log_{10} L)$$

In each component, the supply of suitable habitat, the WUA, is an explicit factor driving a density-dependent population control mechanism: areas of habitat suitable for spawning (AS_{ACT}), fry rearing (AF_{ACT}), and juveniles + adults (AA_{ACT}). By life stage, the WUA is the sum across all habitat units in a lake of the product of the area and suitability of each unit.

In each life stage, the density-dependent mechanisms are assumed to follow a saturation curve. The basic form of the saturation curves uses actual suitable habitat area scaled against predicted ideal requirements to predict proportional achievement of population process rates key to each life stage: actual/(actual + required) declines as the required space increases relative to actual supply. These processes are most often growth or survival rates. As population size increases, the area per animal decreases and the proportional achievement of a potential or maximum process rate declines. As with functional response curves, the shape of the saturation curves may be altered by raising the habitat supply quantities to a power (b) or by scaling the required quantity (a): $\text{actual}^b/(\text{actual}^b + a(\text{required}^b))$. Such a saturation curve can be rearranged algebraically to give a response curve that is a function of the ratio of habitat supplies: $(\text{actual}^b/\text{required}^b)/(\text{actual}^b/\text{required}^b + a)$.

SPAWN: spawning to successful egg deposition and hatching

In SPAWN, the supply of suitable spawning habitat determined the relationship between potential egg deposition and successful hatching of eggs. Potential egg deposition was the product of fecundity, which depends on the length of females in each age-class; the proportion of mature females in each age-class; and the number of females in the age-class, summed across all age-classes. Raat (1988, Table 7) reported several fecundity–length relationships for pike. Three studies (Mann 1976; Bregazzi and Kennedy 1980; Fortin et al. 1982) produced very similar equations. For this model, we applied the average of those three equations, which was obtained by taking separate means of the coefficients:

$$(2) \quad \log_{10} \text{eggs} = -5.238 + 3.527(\log_{10} L)$$

The number of mature females depends on a maturation schedule. We assumed that maturation was size dependent and not age dependent. Changes in adult growth and, thus, size at age affect mean age at maturity. Maturation rarely occurs at a fixed size but is spread over a range of sizes. Both minimum and maximum sizes at maturity were

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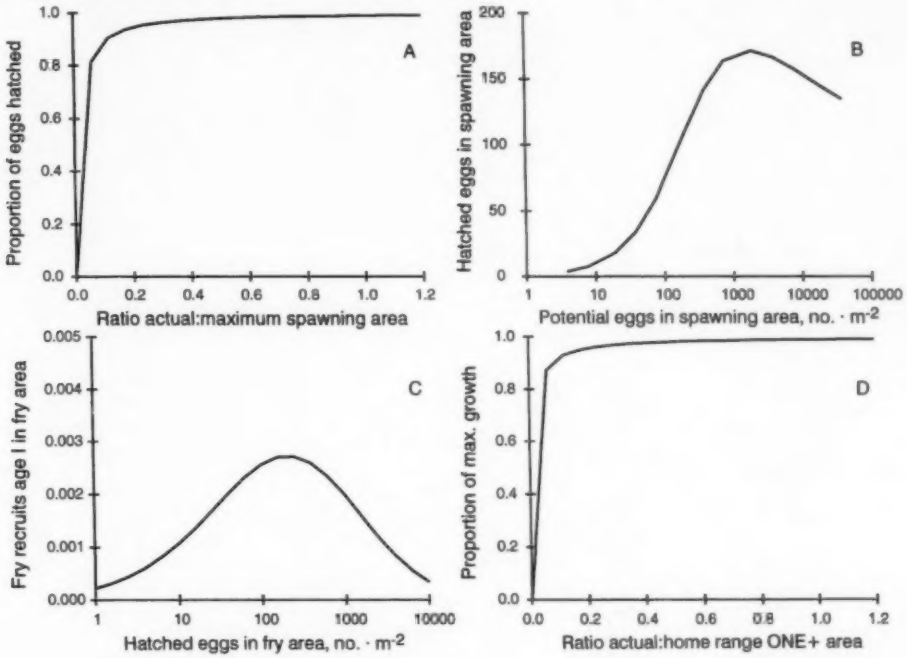
Fig. 2. Graphs illustrating the form of density-dependence mechanisms operating in the three submodels. (A) The proportion of the potential eggs successfully deposited and hatched versus the ratio of actual to maximum spawning habitats. (B) The actual number of eggs successfully deposited and hatched per unit area of spawning habitat versus the potential number. (C) The number of fry recruited at age one per unit area of fry habitat versus the number of hatched eggs in fry habitat. (D) The proportion of maximum growth rate in juveniles and adults versus the ratio of actual to home range ONE+ habitats.


A
Proportion of eggs hatched
Ratio actual:maximum spawning area
B
Hatched eggs in spawning area
Potential eggs in spawning area, no. · m-2
C
Fry recruits age I in fry area
Hatched eggs in fry area, no. · m-2
D
Proportion of max. growth
Ratio actual:home range ONE+ area

defined. If the length was less than the minimum, no fish were mature in the age-class. If the length was greater than the maximum, all fish were mature. In between, the proportion of mature fish rose linearly with size. Summaries of maturation schedules (Raat 1988; Frost and Kipling 1967) indicated that males mature between 300 and 450 mm while females mature between 350 and 500 mm.

In SPAWN, each spawning female was assumed to have minimum and maximum area requirements related to body length. The cumulative sum of minimum and maximum area requirements for all spawning females were computed: AS_{MIN}, minimum spawning area; AS_{MAX}, maximum spawning area. The availability of suitable spawning area (AS_{ACT}) was a submodel input. We then assumed that the proportion of the potential egg supply deposited in habitat where incubation and hatching occur successfully follows a saturation curve relating the spawning area available to the maximum area required by all spawning females. Success decreased as the ratio of the actual spawning habitat supply to the maximum required decreases with increasing numbers of females.

The minimum and maximum spawning areas were assumed to be defined by constant width corridors around the length of the fish (L) with a width equal to multiples of body length (M_{SMIN} and M_{SMAX}):

$$(3) \quad \text{Spawning area per female} = 2(M_{SX})L^2 + \pi(L(M_{SX}))^2$$

where X = MIN or MAX. Larger females require larger minimum and maximum spawning areas. Actual spawning success (SS_{ACT}), the proportion of available eggs successfully hatched, was computed as follows:

$$(4) \quad SS_{ACT} = AS_{ACT}^{sb}/(AS_{ACT}^{sb} + sa(AS_{MAX}^{sb}))$$

where $sa = (1 - SS_{MAX})/SS_{MAX} = 0.0101$ and $sb = \log_e(SS_{MIN}sa/(1 - SS_{MIN}))/\log_e(AS_{MIN}/AS_{MAX}) = 1.11$. The coefficients sa and sb are constant because the area per fish geometry is constant, and only the multipliers differ between minimum and maximum. The saturation curve was force fitted by assuming that proportional spawning success (SS_{MAX}) was 0.99 when the available area equalled the maximum space required (AS_{MAX})and success (SS_{MIN}) was 0.01 when available area equalled the minimum area required (AS_{MIN}). Once the minimum and maximum area requirements had been computed, the coefficients sa and sb were computed and used to calculate spawning success.

Space requirements for pike spawning were difficult to estimate as none of the published literature gave any area estimates. For the minimum spawning area, we assumed the length multiplier, M_{SMIN}, was one; each female required an area with one radius of one body length, an area that is probably too small for the spawning activities. For the maximum spawning area, we examined data gathered in managed pike spawning marshes. Fago (1977) reported the densities of females in managed spawning marshes, giving data for 5 years in one marsh and 2 years for another in Wisconsin. These data were used to calculate area per female. Then, using the inverse of the formula for maximum area per female (eq. 3), the implied multipliers for body length ranged from 65 to 95 with a mean of 80. Data in Franklin and Smith (1963) implied a multiplier range of 42 to 58. In McCarraher (1957), the implied multipliers ranged from 44 to 85. Since these spawning situations were mostly highly managed and involved habitats where both spawning and fry needs are met, we assumed they approximated maximum spawning habitat requirements. Fago (1977) reported 'a rule of thumb' of five females per acre (1 acre = 0.405 ha). The length multiplier, M_{SMAX}, for the maximum spawning area was set at 80.

The proportion of potential eggs that are successfully deposited and hatched increases as the ratio of actual:maximum spawning areas increases (Fig. 2A) following the saturation curve. A hypothetical

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spawning area had varying numbers, 1 – 10 000, of 50 cm length females added, and potential eggs and successful egg hatching per unit area of spawning habitat was computed (Fig. 2B). As the number of spawners increases, the number of hatched eggs rises, but eventually the proportional success rate declines sufficiently that egg success declines as well. The implied egg mortality encompassed the failure of eggs to be fertilized and (or) the mortality of eggs deposited in unsuitable locations and (or) potential overcrowding and mortality of eggs in suitable habitats.

FRY: egg hatch through to recruitment at age one

Growth and survival rates from egg hatch through to recruitment at age 1 were assumed to be inversely related and affected proportionally by the same density-dependent mechanism. This was computed in a single step.

While there were many data relating fry survival to initial egg densities, there were few data relating YOY growth to egg or fry densities. Thus, we were forced to adopt an arbitrary approach to modelling fry growth. Further the methods used to estimate survival from hatched egg to age 1 involved assumptions about fry growth that generated an unresolvable inconsistency between our estimation of survival to age 1 relative to egg density and our approach to modelling fry growth relative to egg density.

There were two compilations of survival data for parts of the time period from 0 (hatch) to age 1: Fago (1977, Table 3) and Wright (1990, Table 5). While some published studies were reported in both data compilations, the data sets were analyzed separately as the independent variables available for analysis differed. In most of compiled cases, the survival data is specific to spawning–rearing habitats. The fish density data for both eggs and fry were assumed to typify values occurring in habitat suitable for fry.

Fago (1977) compiled the results of rearing studies ended at unknown or unreported times, usually within the same season. Variables included: (*i*) initial egg density (*E*; number per square metre) often based on extrapolations from the number of females present and fecundity–size relationships; (*ii*) fry density (*F*; number per square metre) and survival rate (*S*) at the end of the study; and, usually, (*iii*) the mean length (millimetres) of fry at the end of the study. This data set had 46 values. Multiple regression analysis showed: (*i*) $\log_e S$ was inversely related to $\log_e E$ ($r^2 = 0.56$, $P = 0.001$) and (*ii*) $\log_e S$ was inversely related to both $\log_e E$ and $\log_e L$ ($R^2 = 0.61$, $P = 0.001$). The multiple regression equation was

$$(5) \quad \log_e S = 6.306 - 1.104(\log_e E) - 1.816(\log_e L)$$

The egg density coefficient was significantly different from zero at $P = 0.0001$ while that for mean length was at $P = 0.017$. As *E* was the denominator in the estimate of survival, regression correlations might have been overestimated. In a multiple regression with $\log_e F$ as the dependent variable and the regression was marginally nonsignificant ($R^2 = 0.13$, $P = 0.053$). The egg density coefficient was not significantly different from zero while the length coefficient was the same.

These data did not include estimates of survival to age 1, or any time, as experiment durations were not noted. However, if growth in length (*G*) is assumed to be exponential in the first year (cf. Cushing and Horwood 1994), $L_{t=1} = L_{t=0}e^G$ then $\log_e L$ is an approximate estimator of time. If it is further assumed that all fry had the potential to reach the same size after 1 year, the multiple regression can be used to estimate survival to age 1. Visual inspection of size at age data in Raat (1988, Appendix) suggested that a likely upper bound on size at age one was 280 mm. Log_e survival to age 1, $\log_e S_1$, was estimated for the 46 data values as follows by adjusting $\log_e S$:

$$(6) \quad \log_e S_1 = \log_e S - 1.816(\log_e(280) - \log_e L)$$

This produced annual survival rates that ranged, as $\log_e S_1$, from –4.32 to –16.50 with a mean –8.62. Adjusting the survivals by assuming growth to a maximum size at age 1 causes survival rates to be underestimated. No alternative assumption was obvious as a means to obtain estimates of survival to age 1.

In the second compilation, Wright (1990) gathered egg and fry density, and fry survival data along with the duration (time in days) estimated from hatch. Some durations approached a year. This data set included 23 entries. Multiple regression analysis of $\log_e S$ with $\log_e E$, $\log_e T$ (time; days), and $(\log_e T)^2$, produced a significant linear equation ($r^2 = 0.61$, $P = 0.001$):

$$(7) \quad \log_e S = -3.215 - 1.082(\log_e T)$$

Egg density did not enter the regression significantly as $\log_e E$ but was negatively correlated with $\log_e S$. Substituting $\log_e F$ for survival in the regression gave a similar R^2 (0.62) and the $\log_e T$ coefficient was very similar (–1.092). Egg density also entered the regression significantly with a coefficient close to 1 (1.157).

As above, this $\log_e S$ regression equation was used to estimate survival at age 1:

$$(8) \quad \log_e S_1 = \log_e S - 1.082(\log_e(365) - \log_e T)$$

This produced another set of annual survival rates, as $\log_e S_1$, with a narrower range of –7.71 to –13.12 and a lower mean of –9.60 compared with the Fago data set.

The next step was to combine the adjusted Fago and Wright data sets. That data in both data sets came from the same source was not considered a problem as the use of two different adjustment methods effectively created two survival estimates for each overlapping data entry. Before combining the two data sets, it was apparent that survivals from Fago's compilation were generally higher than those in Wright's. Souchon (1983) noted such a disparity in a smaller compilation of studies. He showed that the higher survival rates, typically 10 times the lower ones, were associated with studies where predation effects were excluded through the management of the spawning–rearing area. The Fago data came primarily from highly managed situations while most of the Wright data came from natural, uncontrolled settings. In contrast, our assumption of maximum growth to obtain S_1 values with the Fago data leads to lower survival rates. If lower growth had been assumed, the survival rates would have been higher and the disparity between the Fago and Wright data sets greater. On the basis of Souchon's observation, the Fago $\log_e S_1$ estimates were further adjusted down by subtracting $\log_e(10)$, effectively dividing survival by 10. Then the two sets of $\log_e S_1 + \log_e E$ data were combined.

Visual inspection of a plot of the $\log_e S_1$ versus $\log_e E$ data suggested a modified saturation curve with a density-independent maximum survival rate would describe the relationship; the low range of egg densities coincided with a plateau of survival values. A maximum likelihood function-fitting procedure in RS/1 (BBN 1986) was used to fit the equation:

$$(9) \quad \log_e S_1 = \text{fa} + \text{fb}(E^{\text{fc}})/(\text{fd} + E^{\text{fc}})$$

where fa is the $\log_e$ maximum survival rate, fa + fb is the $\log_e$ minimum survival rate, fc is a power exponent determining the rapidity of the transition between maximum and minimum survival rates relative to egg density, and fd is the egg density raised to the power fc at which $\log_e S_1 = (\text{fa} + \text{fb})/2$. The best fit had an $r^2 = 0.54$ (correlation between observed and predicted $\log_e S_1$ values) with a sample size of 69. The coefficients were as follows: fa = –7.65 ± 3.87 (mean ± SE), fb = –31.73 ± 148.42, fc = 0.31 ± 0.54, fd = 41.70 ± 86.48. These coefficients were used to predict survival from hatched egg to age 1 with egg density calculated as actual hatched egg production divided by the area of suitable fry habitat (AF_{ACT}). As with the analyses of the Fago and Wright data, the r^2 value likely overstated the goodness of fit because egg density is the denominator in the calculation of survival. Alternative approaches to estimating the number of fry at age 1 from hatched egg densities were not considered.

The fry function produced a dome-shaped relationship between hatched eggs per unit fry habitat and fry surviving to age one (Fig. 2C).

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There is considerable evidence of cannibalism among pike fry (cf. Giles et al. 1986). Most mortality occurs in the first weeks after hatch and bimodal size distributions can emerge as the fastest growing fry become consumers of smaller siblings. Such phenomena could produce the fry recruitment patterns simulated here (Fig. 2C).

Having obtained a fry survival model, we sought a comparable growth model. There is strong evidence, particularly among marine fishes (Ware 1975; Pepin 1991), that growth and mortality rates in larval fish are positively correlated. In food-limited situations, higher survival and growth rates are expected with lower densities. In north-temperate freshwaters, overwinter survival of YOY fish often depends on growth in the first summer (Shuter and Post 1990). Failure to achieve a sufficient size because of competition or the lack of suitable habitat during the summer is followed by high mortality in the winter. This phenomenon has a climatic aspect and sustainable yields of northern pike exhibit a dome-shaped relationship with mean annual air temperature (Minns and Moore 1992).

The density-dependent portion of the fry growth model used here was derived from the fry survival model. Fry were assumed to emerge with an initial length of 7.25 mm (Franklin and Smith 1963). A separate length–weight curve ($W = 0.000\ 192\ L^{1.75}$) was used for fry (Franklin and Smith 1963). The maximum length achievable at age 1 was assumed, as above, to be 280 mm. The maximum exponential growth rate, G_{FMAX}, equals $\log_e(280/7.25)$ by definition. Actual fry growth rate was then estimated as follows:

$$(10) \quad G_{FACT} = G_{FMAX}\ fd/(fd + E^{fc})$$

where fc and fd were the same coefficients from the fry survival model. This meant that the fry instantaneous growth rate, G_{FACT}, decreased in direct proportion to decreased survival, $\log_e S_1$, as hatched egg density in fry habitat increased.

The assumptions made for the fry growth model unavoidably conflicted with the method used to obtain estimates of fry survival to age 1 using the Fago data. In the absence of matched growth and survival data for fry over ranges of initial egg densities and fry habitat supply levels, there was no way to avoid the problem. The Fago-derived survival rates were adjusted downwards to make them compatible with the Wright rates. If a lower growth rate had been assumed for the Fago data, the differences between the two sets of survival data would have been even greater, necessitating bigger adjustments. We worked on the assumptions supported by the literature that fry growth and survival rates were both density dependent and coupled. These assumptions remain an untested weak link in this pike model.

ONE+: juveniles and adults

In the ONE+ submodel, annual survival rates were assumed to be constant while growth was assumed to be density dependent.

Raat's (1988, Table 21) compilation of 1+ annual survival data showed that rates are typically in the 35–70% range. There were four studies that reported separate male and female survival rates; male survival was usually less. Mann (1976, 1980), on the Rivers Frome and Stour, and Bregazzi and Kennedy (1980) in Slapton Ley, a small lake, obtained similar survival rates for males and females, 42 and 63 versus 45 and 62. For this model, the male and female annual survival rates for all fish age 1 and older were set at 45 and 65%, respectively.

The sex ratio was assumed to be 50:50 from eggs through to recruitment at age 1. In the model, when fry are recruited at age 1, 50% were placed in each of the age 1 classes for males and females.

The approach to modelling juvenile + adult growth was derivative of and a simplification of the approach used by Walters and Post (1993). They derived a Holling-type disc equation, based on searching for a limited food supply, which was coupled to a Walford-type growth model. They then simplified their approach by assuming that feeding rate was proportional to length raised to the power of two. Here, maximum potential annual growth in length was modelled using equations that empirically describe a linear Walford-type growth:

$$(11) \quad L_{t+1} = G_{OMAX}(1 - L_t/L_\infty) + L_t$$

In such a model, the maximum growth increment (G_{OMax}) is achieved when $L_t = 0$ and is equivalent to the maximum size achieved at age 1. After that, annual growth increments decline in proportion to the ratio of length at any age to the ultimate maximum size, L_∞. The equation for maximum growth is then modified by a density-dependent component.

Fish in natural populations tolerate considerable overlap of home ranges and maximum growth will occur with considerable overlap. Minns (1995) has shown that home range (HR; square metres) in freshwater fish is strongly related to fish size with scalar differences between lakes and rivers:

$$(12) \quad \log_e HR = -2.56 + 3.57Y + 1.52(\log_e L)$$

where $Y = 0$ for rivers and $Y = 1$ for lakes. Home range provided an upper bound to the area of suitable habitat per fish at which maximum growth might be expected to occur. Actual growth is often less than the maximum potential and occurs at typical fish densities. Randall et al. (1995) have shown in natural populations and assemblages that fish density is inversely related to fish size again with consistent lake–river differences. Randall et al.'s equations can be inverted to compute area per fish (square metres) at typical population densities in lakes:

$$(13) \quad \log_e \text{area per fish} = -10.37 + 2.59(\log_e L)$$

Assuming that a proportion of growth potential (G_{OMAX}) was achieved at observed population densities, as in the inverse of eq. 13, allowed the completion of a simple growth model. Using the two size–area relationships, aggregate area demands were estimated for the total 1+ population. We then used those areas to dynamically compute the coefficients in a saturation curve such that 99% of growth potential occurred when the space available equalled the home range space estimate and 50% when the space available equalled the space used by the population according to eq. 13. The growth equation was

$$(14) \quad G_{OACT} = G_{OMAX}(AA_{ACT}^{ob})/(AA_{ACT}^{ob} + oa(AA_{HR}^{ob}))$$

where AA_{ACT} is the actual area available for juveniles and adults, AA_{HR} is the area required if all juveniles and adults occupied non-overlapping home ranges, oa is the scaling coefficient which ensures that $G_{OACT} = 0.99(G_{OMAX})$ when $AA_{ACT} = AA_{HR}$, i.e., $0.99 = AA_{HR}/(AA_{HR} + oa(AA_{HR}))$ (the ob coefficient makes no difference in this calculation), ob is the power coefficient which ensures that $G_{OACT} = 0.50(G_{OMAX})$ when AA_{ACT} is the area required by the population (AA_{POP}) to match that implied by density-body weight relationships for freshwater fish populations in lakes, i.e., $0.50 = AA_{POP}^{ob}/(AA_{POP}^{ob} + oa(AA_{HR}^{ob}))$. The 50% value was an arbitrary choice, selected to produce a size–age relationship consistent with the midrange of values reported by Raat (1988). The coefficient oa is constant and equals 0.0101. The coefficient ob varied with the size–frequency distribution of juveniles and adults because of the disparity of the power coefficients in the home range and population area equations (eqs. 12 and 13). Over the broad range of simulations examined below, the mean value of ob was 0.96 with a range of 0.90 to 1.02. The proportional response of 1+ growth to the ratio of actual to home range areas (AA_{ACT}/AA_{HR}) is shown in Fig. 2D. A high proportion of potential growth is achieved with less than 20% of the required home range area. This result was consistent with the large level of home range overlap implied by eqs. 12 and 13.

Population indices

To show the response of the simulated population to varying levels of habitat supply for the three life stages, several indices were computed for the steady-state populations resulting from 50-year runs (Fig. 1). Population totals were divided by the total lake area to provide a consistent basis for comparison. The indices are (*i*) density (number per hectare) of age 1+ fish before spawning; (*ii*) biomass

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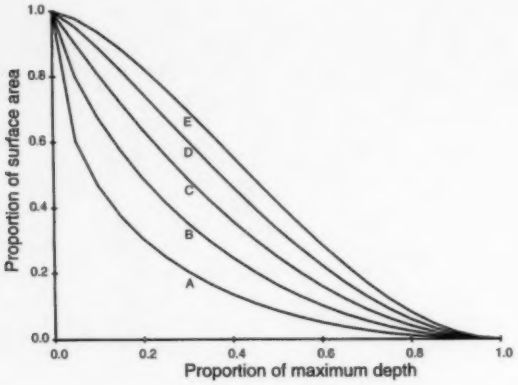
Fig. 3. Hypsographic curves of simulated lake morphometries where the proportion of surface area (A_0) at any depth (Z) is inversely related to the proportion of maximum depth (Z_M) by the equation, $(A_Z/A_0) = (1 - (Z/Z_M)^x)^2$. The five curves result from different values of x: (A) 0.5, (B) 0.75, (C) 1.00, (D) 1.25, and (E) 1.50.



(kilograms per hectare) of age 1+ fish before spawning; (*iii*) mean individual weight (kilograms) of age 1+ fish; (*iv*) successful egg hatching (number per square metre); (*v*) density of fry recruited at age 1 (number per square metre); (*vi*) total annual production (kilograms per hectare per year) of fry, juveniles, and adults; (*vii*) percentage of total annual production by juveniles and adults; (*viii*) production to biomass ratio (*P*/*B*). Annual production was calculated using Ricker's (1975) formulae and the *P*/*B* ratio is based on the mean biomass rather than the biomass before spawning. Production values were calculated separately for the egg hatch to fry recruitment stage and for age 1+ fish and then summed. The percentage of total production due to age 1+ fish was also calculated.

Simulation scenarios

Each simulation runs for 50 years. All population indicators were constant after 40 years and the average indices for the last 10 years were collected from each simulation run. An initial, founding population was generated by assuming an arbitrary size–age structure and running the model with life-stage habitat supplies set equal to the total lake area, 500 ha. No founder effects were evident; changing the initial, arbitrary population numbers and sizes did not affect the size and structure of the simulated population at the end of a 50-year run. The resultant population profile was used as the initial population for all simulation scenarios.

Series 1: comparison of supply limits

In the first series of simulations, the object was to examine how population size and indicators responded to a declining supply of habitat specific to each life stage. The supplies of each of spawning, fry rearing, and juvenile + adult habitats were varied one at a time while the other two were assumed to occupy 100% of the lake area. For each of the three life stages, habitat supply was varied as a percentage of total area in 2% increments from 2 to 98%.

Series 2: varying lake morphometry

As depth ranges have often been reported to define the limits of suitable habitat supply for different life stages of pike, a simplified depth-related model of habitat was assumed for comparative purposes. The areas of SPAWN, FRY, and ONE+ suitable habitat were equated to the areas occupying the 0–0.5, 0.5–2.0, and 1.0–5.0 m depth zones, respectively. Depth ranges of these values were indicated in Inskip (1982) and Minns et al. (1990). In a series of simulations using a 500–ha lake, the maximum depth and the mean:maximum depth ratio were both varied. Varying the maximum depth alters the absolute supply of lake area in each depth range while varying the mean:maximum depth ratio alters the relative supply of areas in each depth range. Lower mean:maximum depth ratios produce a greater extent of littoral area, which in general, is the portion of a lake occupied by pike.

If a lake is assumed to be a cone, the mean:maximum depth ratio is 1:3 and the lake's average radius varies linearly with increasing depth, and therefore, the area is a simple function of depth: $area_Z = A_0 \cdot (1 - Z/Z_M)^2$ (Fig. 3, curve C), where Z is the depth. If the ratio of depth : maximum depth is raised to an exponent, exponents less than one produce lakes with mean:maximum depth ratios less than 1:3 and exponents greater than one produce ratios greater than 1:3. For maximum depths of 5, 10, 20, and 40 m, exponent values of 0.5, 0.75, 1.00, 1.25, and 1.5 were employed, producing a range of hypsometric curves (Fig. 3).

Series 3: Hamilton Harbour

Minns et al. (1993*b*) produced estimates of WUA for northern pike populations in Hamilton Harbour using the modified UET planning methodology. Habitat supply values for the three life-stage groupings were estimated for three scenarios: original, the pristine, pre-1800 ecosystems; current, the current, highly degraded ecosystem; and restored, an expected future state of the ecosystem with many habitat features restored and expanded. Depth, vegetation, and water-quality factors were integrated via a geographic information system based representation of Hamilton Harbour to produce WUAs for spawning, fry rearing, and juvenile + adult groupings. Population simulations were run for these three scenarios using the estimated areas.

In addition, a series of reference and comparative simulations was also run. First, the baseline simulation predicted the pike population obtained if the habitat supply for each life stage was equal to the area of Hamilton Harbour. Second, the simplified morphometric habitat supply used in series 2 scenarios was also applied. The original area of 3081.24 ha (Minns et al. 1993*b*) and the maximum depth of 26 m were used in the simulation with the same series of mean:maximum depth ratios used in the morphometric scenarios.

Results

Once all the equations were assembled into computation procedure, no calibration was required to make the model operational. The parameter values for the pike simulation model are summarized in Table 1.

Series 1: comparison of supply limits

All the population indicators were affected by restrictions on the habitat supply for each life stage (Figs. 4 and 5). Density declined most rapidly with the level of fry habitat and persisted at high levels over much of the range of spawning habitat (Fig. 4A). Biomass declined rapidly, and almost identically, with fry and juvenile + adult levels (Fig. 4B). However, mean weight of age 1+ pike increased with lower levels of fry habitat, decreased with lower levels of 1+ habitat, and remained relatively unchanged over most of the supply range until rising with very low levels of spawning habitat (Fig. 4C). Total production responses largely paralleled those of biomass though the decline with 1+ habitat was slower than with fry habitat (Fig. 4D). Successful egg deposition declined in a similar manner to density (Fig. 5A) with 1+ habitat producing the fastest decline and spawning the slowest. Fry recruitment at age 1 also followed the same pattern as density with fry habitat

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Fig. 4. Comparative response of four pike population indicators: (A) density (no.·ha^{-1}); (B) biomass (kg·ha^{-1}); (C) mean weight of age 1+ fish (kg); and (D) production kg·ha^{-1}·year^{-1}, to a varying supply, as a proportion of total lake area, of habitat suitable for each of three life stages: SPAWN, solid line; FRY, broken line; ONE+, dotted line.

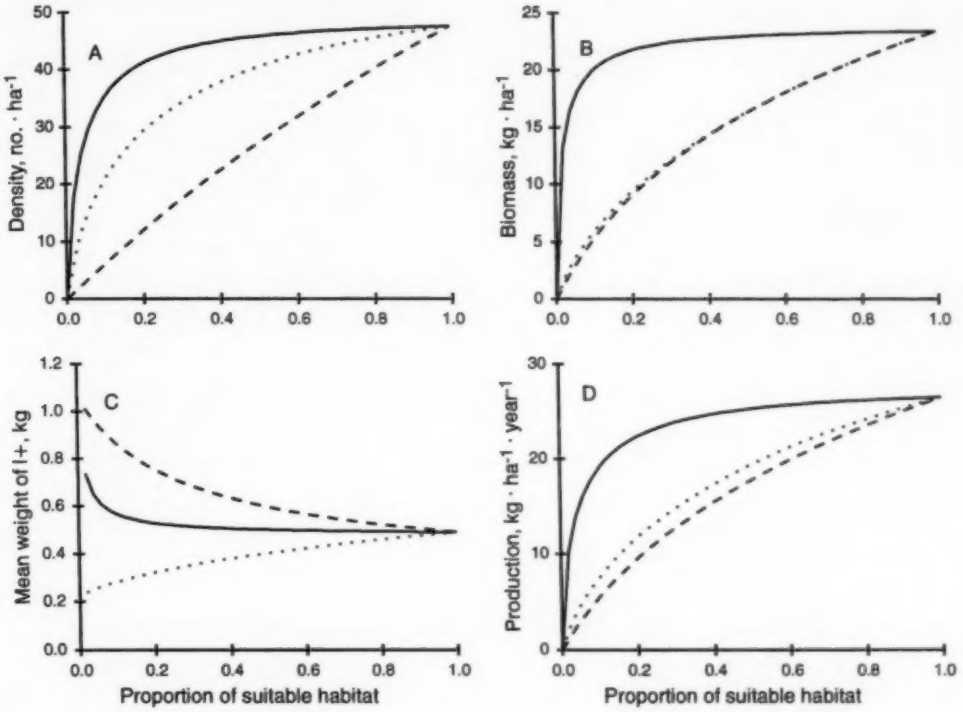

Table 2. Summary of responses in population indicators to restrictions on habitat supply to each life stage; the arrows show the direction of change and their number gives a relative qualitative indication of the degree of response.

	Effect of restricted habitat supply		
Population indicator	Spawn	Fry	One+
Density	↓	↓↓↓	↓↓
Biomass	↓	↓↓↓	↓↓↓
Mean weight	↑	↑↑	↓
Production	↓	↓↓↓	↓↓↓
Egg deposition	↓	↓↓	↓↓↓
Fry recruitment	↓	↓↓↓	↓↓
% ONE+ portion of production	↑↑	↑↑	↓
P/B ratio	↓↓	↓↓	↑

producing the most rapid decrease in recruitment (Fig. 5B). The percentage contribution of juveniles and adults to total production increased with declines in fry and spawning habitat but decreased with lower levels of 1+ habitat (Fig. 5C). Consistently, the *P/B* ratios showed the opposite pattern to the percentage of production due to juveniles and adults (Fig. 5D); smaller, younger life stages show a greater *P/B* than older, large ones.

The trends among the eight population indicators can be summarized (Table 2). Given equal proportions of lake area providing suitable habitat for each life stage, restrictions on spawning habitat usually had the least influence while restrictions of fry habitat generally invoked the strongest responses. The responses to juvenile–adult habitat restrictions were usually more similar to the fry responses. Mean weight and percentage juvenile–adult production decreased in response to 1+ habitat restrictions while increasing with spawning and fry habitat restrictions.

For comparative purposes, size and age composition were examined when all life-stage habitat supplies equal lake area (Fig. 6A), and when a level of habitat restriction for each life-stage is selected (Figs. 6B–6D) to produce a population biomass about half that in the reference scenario (Fig. 6A). Those habitat supply values equalled 2, 30, and 28% of lake area for SPAWN, FRY, and ONE+, respectively. The simulated population structures exhibit apparently anomalous upward trends in numbers and length at age 10 (Fig. 6). These are artifacts of the simulation process, which restricts the number of age-classes to 10 and requires that every year, a newly generated 11th age-class of fish be averaged back into the 10th age-class. Since the 10th age-class is only a small percentage of the steady-state population, the numerical impact on the simulation outcomes and the population indicators is small. The overall smoothness of the numbers and length-at-age curves reflects the simplicity of the underlying model assumptions, i.e., constant juvenile and adult mortality rates and Walford-like growth.

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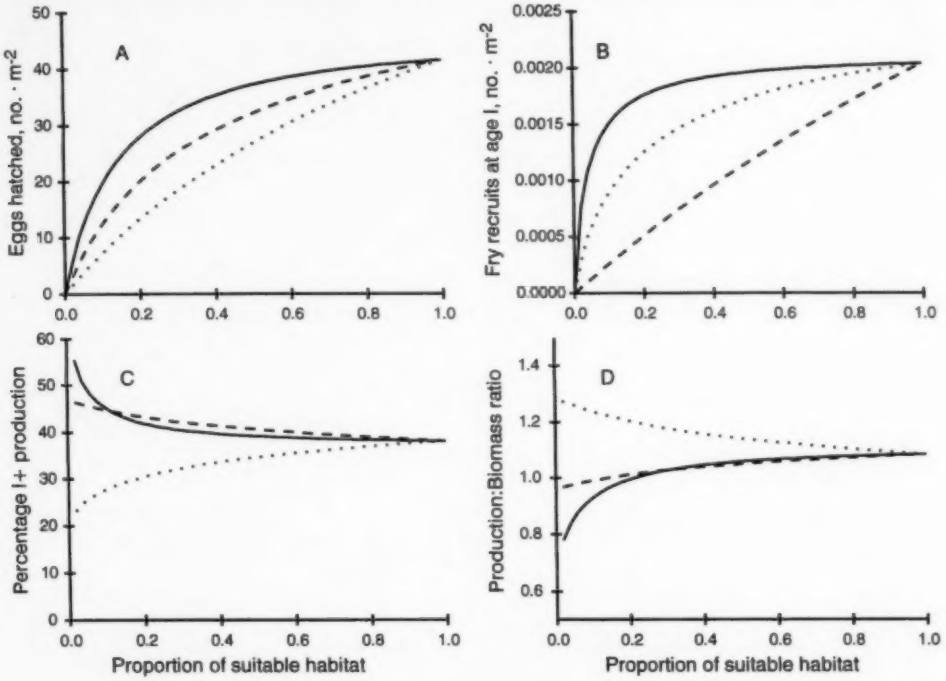
Fig. 5. Comparative response of four pike population indicators: (A) eggs deposited and hatched (no.·m^{-2}); (B) fry recruitment (no.·m^{-2}); (C) juvenile + adult production as percentage of the total, and (D) Production/biomass ratio, to a varying supply, as a proportion of total lake area, of habitat suitable for each of three life stages: SPAWN, solid line; FRY, broken line; ONE+, dotted line



When restrictions on each life-stage habitat supply were imposed to produce approximately a halving of biomass, differences in population structure were evident (Fig. 6). The numbers of animals in all age-classes were reduced but less so when ONE+ habitat was restricted (Fig. 6D). With SPAWN and FRY habitat restrictions, length-at-age increases (Figs. 6B and 6C) while decreasing with ONE+ habitat restriction (Fig. 6D). Initial size at age one increased when FRY habitat was restricted (Fig. 6B). These results indicate that habitat supply limitations can be diagnosed using population response indicators.

Series 2: varying lake morphometry

Simulations with various lake morphometries and maximum depths, assuming that depth ranges define life-stage habitat supplies, showed clear trends. First, as maximum depth increased, the total population density and biomass generally declined although mean weight increased (Table 3); as maximum depth increases less of the total lake area is suitable for most pike life stages. With mean:maximum depth ratios, there was an interaction with depth. At lesser maximum depths, 5 and 10 m, the maximum population biomass and production values occurred at intermediate depth ratios (Table 3). At greater maximum depths, 20 and 40 m, maximum biomass and production occurred with the lowest depth ratios (Table 3). These results are caused by differential shifts in the proportions of habitat supplied; at shallower depths, habitat for the ONE+ stage increases with the depth ratio as habitat for the SPAWN stage decreases. With each maximum depth value, the mean size of pike increased with the mean:maximum depth ratio while egg hatching rates, fry recruitment densities and *P/B* ratios declined (Table 3).

Series 3: Hamilton Harbour

The series of simulations for Hamilton Harbour show both the influence of morphometry and the potential for restoration relative to the original ecosystem state (Table 4). The baseline model run with no habitat limitations gives the same unit area results as in series 1 and 2 baseline runs; total area does not affect unit area results. The simplified morphometric simulations produce populations with a biomass range 6.3–1.3 kg·ha^{-1} and a production range 6.9–1.1 kg·ha^{-1}·year^{-1}, declining with increasing mean:maximum depth ratio. The UET-based (Minns et al. 1993*b*) scenarios produce a similar range of biomass and production.

Based on the patterns seen in the first group of simulations, the shifting proportions of habitat in the UET scenarios for Hamilton Harbour indicate (*i*) FRY habitat in the original scenario and (2) ONE+ habitat in the current and restored scenarios were limiting. The UET assessment of overall habitat limitations based on experts assigned weights of 0.456, 0.297, and 0.247 for SPAWN, FRY, and ONE+ life stages, respectively (Minns et al. 1993*b*), implying that spawning habitat is limiting. The different scenarios also show how the mechanism limiting a population can changes with differential shifts in habitat supply.

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Fig. 6. Comparisons, at steady state, of simulated pike population structure, number (lines moving down from left to right in each panel) and length (mm) (line moving up from left to right) by age (1–10) and sex (males, solid lines; females, broken lines), in four habitat supply scenarios: (A) baseline with SPAWN, FRY, and ONE+ habitat areas equal to total lake area (500 ha), (B) with SPAWN equal to 2% of lake area, (C) with FRY equal to 30% of lake area, and (D) with ONE+ equal to 28% of lake area. Scenarios B, C, and D produce pike populations where biomass is approximately half the baseline value.

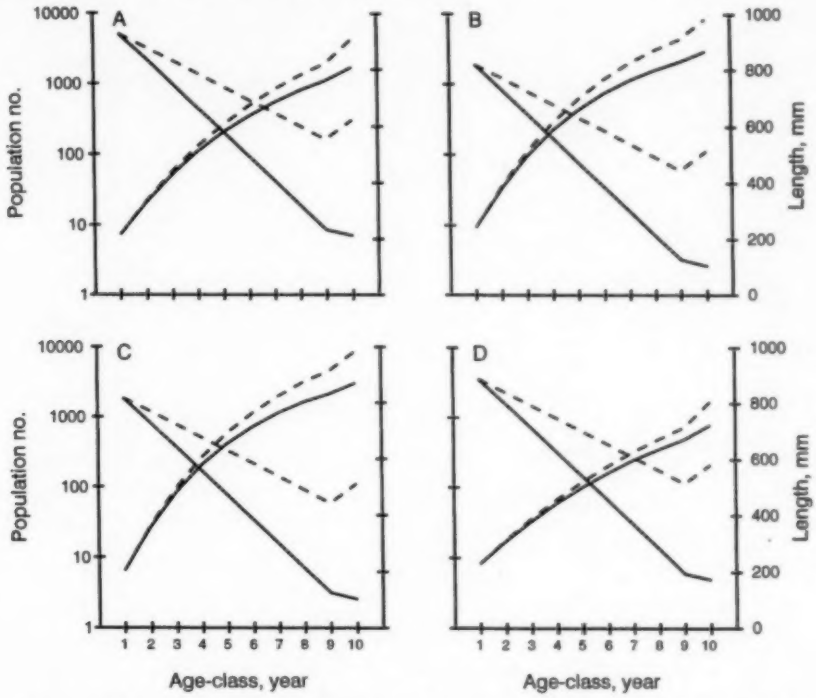

Table 3. Simulated pike populations resulting from assumed maximum depths and mean:maximum depth ratios in a 500-ha lake, showing the proportions of suitable habitat for each life stage and the population indices.

Depth		Proportion of habitat			Population indices							
Max.	Mean/max.	Spawn	Fry	One+	Density (no.·ha^{-1})	Biomass (kg·ha^{-1})	Min. wt.(kg)	Production (kg·ha^{-1})	Eggs (no.·m^{-2})	Fry (no.·m^{-2})	% 1+ production	*P/B* ratio
—	—	1.000	1.000	1.000	47.67	23.46	0.492	26.54	41.54	0.00204	38.0	1.09
5	0.167	0.532	0.332	0.306	15.81	7.53	0.476	8.67	13.71	0.00068	37.2	1.10
5	0.257	0.324	0.429	0.491	20.70	10.68	0.516	11.83	18.48	0.00089	39.1	1.06
5	0.333	0.190	0.450	0.640	21.57	12.12	0.562	12.77	19.00	0.00092	41.5	1.02
5	0.397	0.109	0.426	0.750	19.78	12.17	0.615	12.06	16.41	0.00085	44.4	0.96
5	0.450	0.062	0.380	0.829	16.61	11.25	0.677	10.41	12.43	0.00071	47.9	0.91
10	0.167	0.397	0.297	0.382	14.97	7.90	0.528	8.84	14.63	0.00064	39.0	1.07
10	0.257	0.200	0.308	0.512	15.65	9.05	0.578	9.65	15.54	0.00067	41.3	1.03
10	0.333	0.098	0.262	0.560	13.11	8.33	0.636	8.38	12.56	0.00056	44.1	0.98
10	0.397	0.047	0.203	0.555	9.71	6.80	0.701	6.39	8.53	0.00042	47.5	0.92
10	0.450	0.022	0.149	0.520	6.63	5.11	0.771	4.48	5.12	0.00028	51.1	0.86
20	0.167	0.291	0.241	0.353	12.37	6.79	0.549	7.51	12.59	0.00053	39.7	1.06
20	0.257	0.122	0.202	0.382	10.39	6.25	0.602	6.58	10.62	0.00044	42.1	1.01
20	0.333	0.049	0.141	0.340	7.07	4.67	0.660	4.63	6.89	0.00030	45.0	0.96
20	0.397	0.020	0.090	0.276	4.30	3.11	0.725	2.88	3.80	0.00018	48.3	0.91
20	0.450	0.008	0.054	0.212	2.42	1.92	0.793	1.66	1.87	0.00010	51.9	0.85
40	0.167	0.211	0.186	0.291	9.62	5.39	0.561	5.92	9.98	0.00041	40.1	1.05
40	0.257	0.073	0.127	0.254	6.55	4.02	0.613	4.19	6.78	0.00028	42.5	1.01
40	0.333	0.025	0.073	0.185	3.66	2.46	0.671	2.42	3.59	0.00016	45.3	0.96
40	0.397	0.008	0.038	0.123	1.84	1.35	0.733	1.24	1.63	0.00008	48.6	0.90
40	0.450	0.003	0.019	0.079	0.87	0.69	0.800	0.60	0.67	0.00004	52.1	0.85

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Table 4. Simulated pike populations in Hamilton Harbour resulting from no habitat limits, simple depth range–life stage limits, and habitat limits derived from UET weighted-usable area assessments in three scenarios.

	Area (ha)	Min./max. depth ratio	Proportion of habitat			Population indices							
			Spawn	Fry	One+	Density (no.·ha^{-1})	Biomass (kg·ha^{-1})	Min. wt. (kg)	Production (kg·ha^{-1})	Eggs (no.·m–2)	Fry (no.·m^{-2})	1+ production (%)	*P/B* ratio
No habitat limits (baseline)													
	3081.24	—	1.000	1.000	1.000	47.67	23.45	0.492	26.54	41.53	0.0020	38.0	1.09
Simple life-stage depth limits with various mean/max. depth ratios													
	3081.24	0.167	0.258	0.220	0.331	11.30	6.27	0.554	6.90	11.61	0.0005	39.8	1.06
	3081.24	0.257	0.101	0.170	0.330	8.76	5.32	0.607	5.57	9.01	0.0004	42.2	1.01
	3081.24	0.333	0.038	0.110	0.272	5.53	3.68	0.665	3.63	5.40	0.0002	45.1	0.96
	3081.24	0.397	0.014	0.065	0.205	3.13	2.28	0.729	2.10	2.76	0.0001	48.5	0.90
	3081.24	0.450	0.005	0.037	0.147	1.65	1.31	0.796	1.13	1.27	0.0001	52.0	0.85
UET weighted usable area scenarios													
Orig.	3081.24	0.325	0.225	0.198	0.315	10.25	5.78	0.564	6.33	10.71	0.0004	40.1	1.05
Curr.	2300.14	0.438	0.068	0.083	0.031	3.04	1.14	0.375	1.37	1.78	0.0001	33.4	1.16
Rest.	2291.23	0.439	0.100	0.104	0.098	4.89	2.37	0.484	2.69	4.15	0.0002	37.8	1.09

Discussion

The northern pike population model and resulting simulations are considered in four ways: (*i*) the limitations of the model and its parameters; (*ii*) the relationship to other fish population models; (*iii*) the significance of the results, particularly in Hamilton Harbour, and their implications for fish habitat management; and (*iv*) the future potential developments and applications. This is followed by some conclusions.

Model and parameter limitations

This model provides a generic representation of northern pike population dynamics. Since pike populations from the north temperate region of North America were the source of many of the equations and parameter values, the resultant model most likely simulates an average population in that region. The pike population density and biomass values generated in the series 1 scenarios overlap most of the range of values reported from lakes (Raat 1988). Higher values reported for shallow mesotrophic lakes in the Netherlands (Grimm 1981) were a noticeable exception. Size-at-age patterns obtained with the simulation model are in the middle of the range of growth curves reported in wild populations (Raat 1988).

Each equation in this northern pike population model is a possible source of error and can influence the pattern of response in the population indicators. In all cases, both the equation form and the particular parameter values might be challenged. There are three types of equations in the model: (*i*) allometric ones such as length-weight, fecundity-length, and home range-length; (*ii*) functional ones such as juvenile and adult annual survival rates and sexual maturation schedules, which are not directly affected by changes in population size and (or) habitat supply; and (*iii*) functional ones such as egg deposition, fry survival, and adult growth, which are density or habitat supply dependent. The first two types of equations are easily obtained from literature while the third is not.

Allometric and functional equations are less likely to be challenged as relationships such as length–weight (eq. 1) and fecundity–length (eq. 2) are well established and widely measured. For instance, we used Willis' (1989) standardized length–weight equation for pike, recognizing that the relationship can vary from place to place. Because weight does not enter directly into most model equations, changing the length–weight equation parameters would only affect mean weight, population biomass, and production values, which are computed from population numbers and lengths by age-class. Fecundity–length equations vary in form (Raat 1988) but the logarithmic form (eq. 2) is the most widely used. Increased fecundity would increase the number of eggs hatching and would be offset by increased mortality of fry. Using a size-based sexual maturation schedule causes age at maturity to be affected by changes in growth. Available literature data on pike (Raat 1988) suggests that size-at-maturity is relatively more constant than age-at-maturity.

Population density or habitat area dependent functional equations are potentially the most controversial components of the model. These model equations were chosen to provide empirical, descriptive representations of habitat supply-dependent effects. No attempt was made to derive equations on the basis of causal explanations. However, saturation curves were chosen for both theoretical and practical reasons. On the theoretical side, saturation equations are often used to model biological processes and have been derived from first principles (Taylor 1984; DeAngelis et al. 1975). Michaelis–Menten equations are an example of a saturation curve and were developed to describe enzyme kinetics. Algebraically similar equations, e.g., Holling's disc equation and Monod's formula, have been used to describe, respectively, consumption of prey by predators and bacterial growth in chemostats (Taylor 1984). Generally, saturation equations depend on the levels of both consumers and consumed with a saturation effect occurring in response to increasing consumer levels for a given level of consumed. This characteristic pattern is expected to occur when the number of fish occupying available, suitable habitat approaches and exceeds the carrying capacity.

There are practical reasons for using saturation equations. First, it is easy to separate the absolute response variable from proportional part of the equations. For example in ONE+, maximum potential growth increment was modelled using a

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Walford-type equation while the proportional achievement of that potential depends on the supply of ONE+ habitat relative to demand. Second, the formulas include a constant component that equals the area or density at which half the proportional response is achieved. Third, where data do not exist to estimate the coefficient values in the equation, the saturation functions can easily be scaled to produce preferred or expected levels of proportional response at prescribed densities or habitat supply levels. Among habitat-related functional equations, that for fry survival is the best grounded in available data though all have weaknesses.

In SPAWN, spawning requirements were a simple geometric function of female length. There were no exact data to guide the specification of both minimum and maximum spawning areas. However, spawning success will vary with the size of spawning area available and the number of spawning females. Crowding in suitable habitat may cause reduced hatching rates or cause surplus spawners to deposit eggs in unsuitable habitats where hatching rates are lower or zero. The data used to estimate maximum spawning area multiplier came from spawning marshes and most likely overestimated the area required. The minimum multiplier was simply chosen to be less than that suggested by anecdotal knowledge of the spacing between spawning females. True maximum spawning area requirements are likely less than those used in the model. This implies that spawning habitat is less limiting if the area required per female is smaller.

In FRY, the functional relationship for survival was based on an assembly of data. Again, as with SPAWN, spawning marsh results dominated and there is a risk that egg densities per unit of suitable fry habitat are underestimated. In the model, this error would cause survival rates to decline sooner at low egg densities and, therefore, might cause fry recruitment to be underestimated. The reciprocal assumption of fry growth being inversely related to survival was untested and was inconsistent with the methods used to adjust and pool the fry survival rate data. However, the linkage of survival and growth rates was consistent with the expected relationship for YOY fishes (Ware 1975; Pepin 1991).

In ONE+, the model was formulated using the consensus view (Shuter 1990) that growth rates are often density dependent while survival rates are density independent in juvenile and adult fish. Area per fish at observed population densities and home range area provided realistic bounds for inferring changes in juvenile and adult growth rate. Since fish home ranges overlap significantly, maximum growth should be attained when suitable habitat area per fish matches the home range size. Fish will attain average growth rates at average population densities. This approach provides an empirical equivalent of the bioenergetic approach to modelling growth outlined by Walters and Post (1993).

Since the suitable habitat supply values are fixed inputs to the model, representing aggregate WUAs, many habitat features cannot be represented. The aggregation ignores the habitat fragmentation, connectivity, and contiguity issues that are central to conservation (Scott et al. 1993). The aggregation of WUAs also means that any inequalities of gain attributable to differing levels of suitability in separate habitat units are ignored. The WUA approach implicitly assumes that an ideal-free distribution (Fretwell and Lucas 1970) of fish is achieved with the suitabilities equalling the proportional densities expected in each discrete unit of habitat.

The pike model is deterministic and, therefore, cannot reflect external variability that could affect both the values of input parameters and (or) the life-stage habitat supplies. Use of average size for each age-class precludes the level of detail incorporated in individual-based models (IBMs) (Tyler and Rose 1994).

Relationship to other fish population modelling

Fish population models with explicit links to some aspects of habitat can be simple or complex. The pike model developed here is most like the simple models. There are several examples of relatively conventional fish population modelling where a simple aggregate approach to habitat has been taken (Frisk et al. 1988, whitefish (*Coregonus* sp.) in relation to water level fluctuations; Cheslak and Jacobson 1990, rainbow trout (*Oncorhynchus mykiss*) in an instream flow incremental method (IFIM; cf. Bovee 1982) extension; and Ogawa and Mitsch 1979, gizzard shad (*Dorosoma cepedianum*) in a river with power plant impacts imposed). Schaaf et al. (1987, 1993) and Shuter (1990) have used highly simplified population models and examined how bottlenecks at various life stages affect population size and structure. The simple models provide insights into the relative influence of various habitat factors and population processes.

More recently, geographic information systems technology has made it possible to explore the many features and layers of habitats. Complex mosaics of habitat units emerge when only a few habitat features are overlaid. These mosaics prompted suggestions that complex spatially explicit and possibly IBMs will be required to simulate such populations in heterogeneous environments. For instance, Van Winkle et al. (1993) developed such IBM models for smallmouth (*Micropterus dolomieu*) and striped bass (*Morone saxatilis*) to examine the impact of altering fry habitat supply. Many articles cited in the Tyler and Rose (1994) review suggest that spatially explicit IBMs are needed if outstanding fishery resource management issues are to be resolved. However, as Tyler and Rose point out, the data and process understanding requirements of such models are enormous. Williamson et al. (1993) provide a conceptual outline for such a model involving a salmonid population in an IFIM context. Little prior empirical knowledge is available to guide the formulation of such complex models. In both simple and complex models, the representation of habitat supply has generally been minimal. Judging by the Tyler and Rose review, we think simpler fish population – habitat models that represent cohorts of fish and operate with explicit, aggregate measures of habitat supply have received insufficient attention.

Significance and implications of results

Our population modelling approach effectively links two approaches to fish ecology: (*i*) a dynamic one concerned with the responses of population size and structure to density-dependent mechanisms and (*ii*) a static one concerned with the quantitative relationship between habitat supply and population size. Series 1 simulations comparing supply limits show that the absolute supply of suitable habitat specific to a life stage is not a reliable guide to its importance to population size and productivity. Habitat supply must be compared with demand

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to establish whether a particular habitat is limiting for a population. Of course, all life-stage habitats are essential to the completion of a population's life cycle. The percentages of total habitat supply producing half the reference population biomass show (Fig. 4) how misleading absolute areas specific to life stages can be when assessing relative importance to population conservation. Spawning areas are often perceived to be a small part of the lake area but only a small area may be required. Fry, juvenile, and adult fish need larger absolute areas. Incremental absolute losses of FRY or ONE+ habitat have a greater impact at almost any level of supply while losses of spawning habitat only produce greater proportiooal losses of population size when the absolute supply is very low.

Series 2 simulations of varying lake morphometry show that habitat suitability can be represented in the simplest of forms. In lakes, depth profiles and accompanying thermal regimes have a major controlling effect on fish populations (Magnuson et al. 1979; Christie and Regier 1988). By assuming that all regions of a lake within prescribed depth ranges were suitable, we probably overestimated the supply of suitable habitat. However, the overlap of the range of results with observed population characteristics suggests that further analysis of the hypsometric curves in lakes might explain some of the variation in the size of pike populations.

In the Series 3, Hamilton Harbour, simulations, planned habitat restoration activities, and hindcasts of original habitat supply were linked to predictions of population size and structure. Support for habitat restoration measures will be strengthened if, in addition to giving a measure of improved habitat supply, biologists can estimate the increased size of fish populations.

In Hamilton Harbour, the ecosystem area has decreased from 3081 to 2300 ha. Unit-area population indices hide the effect of loss of area. Using the simulation results, production has declined from 19 500 to 3150 kg·year^{-1} between the original and current scenarios and increases to 6160 in the restoration scenario. Current production is 16% of original and restored 32% of original. If maximum sustainable yield (MSY) is 50% of ONE+ production (40% of total production), i.e., when fishing mortality equals natural mortality, potential yield in the original scenario is 3900 kg·year^{-1}. Beddington and Basson (1993) quote Gulland's estimator of MSY as $0.5MB_0$. In the original scenario, Gulland's formula gives a value of 5340 kg·year^{-1}. These figures are comparable with, but lower than, fishery yields of 15 000 – 20 000 lbs, or 6800–9090 kg, reported in Hamilton Harbour during the 1871–1901 period (Holmes and Whillans 1984). As the fisheries declined toward the end of the last century, those actual yields may have exceeded the MSY limit such that overexploitation compounded the effects of habitat loss and degradation. In addition, as the harbour is connected to Lake Ontario, immigration and emigration of pike and their forage could have affected pike productivity and harvest.

The altered morphometry of Hamilton Harbour has accounted for some of the change in biomass and production. In the UET scenarios, the mean:maximum depth ratio has changed from 0.325 to 0.438 (Table 4) as large areas of shallow littoral habitat were filled during industrial development of the harbour. Similar changes in the simplified depth range simulations produced comparable changes in biomass and production. Mean weights increase in the simplified scenarios but change little in the UET scenarios because poor water quality severely limits the supply of suitable juvenile + adult habitat.

The results in the three series of simulations show that progress toward resolution of fish habitat restoration, conservation, and protection priorities can be made via this simple modelling approach. The results also show how HEP- and UET-based aggregations of suitable habitat can provide a practical, more widely applicable basis for linking habitat to the established approaches to assessing and analyzing population dynamics.

Shuter's (1990) cogent analyses showed how fry and adult bottlenecks in fish populations can generate differences in population indices. The pike model has three bottlenecks, adding spawning to the two discussed by Shuter. Only one of the bottlenecks can limit population size at any time although the relative proximity of the population's habitat demands to the supply limits probably affects some of the population indicators. Changes in recruitment and growth patterns seen in the pike simulations follow Shuter's expectations.

Future potential developments and applications

Development and application of this simple modelling approach can be expanded in many ways. On the development side, the effects of variability need to be assessed. Parameter values in model equations are uncertain and the supplies of habitat might also be variable. As variability increases, the likelihood of population extinction increases (cf. Soulé 1987). Additional population indicators assessing population viability might be needed. The impact of exploitation should be examined in relation to variability. Harvesting in the presence of parameter or habitat supply uncertainties may further increase the likelihood of extinction.

The applicability of the model might be extended by incorporating adjustments of some parameters to reflect gradient effects evident across the species range, e.g., variations in maximum growth rates with climate. The HEP and UET measures of suitable habitat generally assume that location in the species range is unimportant. Shuter and Post (1990) and Minns and Moore (1992) have shown how fish population success can vary regionally. The modelling of life-stage bottlenecks by Shuter (1990) suggests that key life-stage rate processes will vary across a species range. These effects will condition life-stage interactions and lead to differential changes in the impact of habitat supply limits.

Our modelling approach can be extended to other species and might allow predictions of multispecies assemblage composition and structure. Such an extension would require the development of a simple method of measuring interspecies overlaps of suitable habitats and including their effect in the density-dependent functional equations. Here, both competitive and predator–prey interactions with other species have been ignored. Competitive interaction might be modelled by assessing the degree of overlap in suitable habitat requirements for different life stages and then using a weighting approach to factor the abundance of other species into existing density-dependent mechanisms. Predator–prey effects could be simulated by adding mortality rates weighted by overlap of habitat use. Spawning and fry habitat usage is often segregated in time and space while juvenile–adult habitat usage often has large overlaps. Theoretical analysis suggests that the partitioning of assemblage biomass and production among species is

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strongly related to the partitioning and layered use of suitable habitats (Kolasa and Strayer 1988; Kolasa 1989).

Conclusions

Concern is increasing about the cumulative effects of fish habitat degradation, fragmentation, and loss. Efforts to sustain populations through the conservation of habitat are often concentrated on habitats considered to be rare, critical, or in short supply. The pike modelling results strongly suggest that intuition may be an unreliable guide to such habitats and is based on an incomplete assessment of a population's needs. Protection of small areas while neglecting larger areas may be a serious error. Pulliam and Danielson (1991) have shown with simple models of two-stage populations in categorical habitat mosaics that "source" habitats provide the surplus of production but "sink" habitats are needed if the whole population is to persist. In essence, incremental losses of habitat that seems marginal to humans can have negative consequences to the fish population. Simplistic approaches that try to reconcile human encroachment on habitats with the maintenance of fish community composition and potential yield assume large areas of habitat can be eliminated or degraded without significant fisheries implications. That wishful thinking is challenged by the results of this pike modelling study and similar efforts. Tilman et al. (1994) presented a model of communities of metapopulations in ecosystems of habitat patches. Their simulations indicated that incremental habitat loss caused extinctions with the most dominant species being the most vulnerable with long time delays. The link between past losses of habitat and current extinctions may not be obvious. Extinctions occur in rank order. That outcome is consistent with the model of community composition proposed by Kolasa and Strayer (1988) and Kolasa (1989). The species with the greatest abundances occupy the greatest proportion of habitat patches while less abundant species occupy fewer patches. Random loss of habitat patches will adversely affect populations making more extensive demands of the total habitat supply.

Increasingly, fishery managers are being confronted with situations where exploitation, invasions, and habitat modification and destruction are co-occurring with potentially disastrous implications for fish populations and assemblages. Successful conservation of fish resources will require that the two research arenas (population dynamics and habitat supply and demand) converge and merge; sustainable use of fish requires limits to exploitation, minimal disturbance with exotics, and protection of all the habitats needed to support fish biodiversity and production.

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We want to especially note the inspirational role of Shuter's (1990) and Kozlowski's (1985) papers in the genesis of this model. The continuing development and implementation of the Remedial Action Plan in Hamilton Harbour has generated a demand for predictions of the ecological, especially fish, benefits to be realized through habitat restoration. We are motivated by our desire to meet this need. The comments of the three referees aided the preparation of this final version.

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The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes

R.G. Randall, C.K. Minns, V.W. Cairns, and J.E. Moore

Abstract: An index of fish production was significantly higher in littoral habitats with abundant submerged macrophytes, as measured by percent bottom cover, than in adjacent areas with low macrophyte abundance. Plots of fish abundance versus fish size showed that vegetated sites had higher densities of fish, smaller fish, and greater species richness than unvegetated sites. Using information on fish biomass (B) and fish size (W), a production index (PI) was calculated as $\log_{10}$ PI = $-0.35 \log_{10} W + 0.90 \log_{10} B$. The production index was significantly related to macrophyte density, phosphorus, slope of the littoral area, and fish species richness. The regression model explained 61% of the variability in PI if species richness was included but only 43% if habitat features alone were used. Fish numbers decreased, and conversely fish size increased, with increasing littoral slope and maximum exposure. Species richness was correlated with effective fetch, but in a nonlinear manner. Methods for increasing the precision of models for estimating fish production in littoral habitats are suggested. Conservation should be directed at protecting not only the productive vegetated littoral habitats but also adjacent areas which benefit from the high productivity as well.

Résumé : L'indice de production de poissons que nous avons choisi pour la présente étude avait une valeur considérablement plus élevée dans les habitats littoraux où les macrophytes submergées sont abondantes (en termes de pourcentage de couverture du fond) que dans les zones voisines où ces plantes sont peu abondantes. En positionnant les habitats sur un plan de coordonnées correspondant respectivement à l'abondance des poissons et à leur taille, nous avons constaté que la densité des poissons et la richesse en espèces étaient plus élevées dans les habitats à végétation abondante que dans les habitats dénudés; cependant, la taille des poissons était moindre. A partir de mesures de la biomasse (B) et de la taille (W) des poissons, nous avons calculé un indice de production PI tel que $\log_{10}$ PI = $-0{,}35 \log_{10} W + 0{,}90 \log_{10} B$. La valeur de cet indice était reliée de façon significative à la densité des macrophytes, au taux de phosphore, à la pente de la zone littorale et à la richesse en espèces de poissons. Le modèle de régression utilisé permettait d'expliquer 61 % de la variabilité du PI si on tenait compte de la richesse en espèces, mais seulement 43 % de cette variabilité si on se limitait aux caractéristiques de l'habitat. Le nombre des poissons diminuait, et leur taille augmentait, avec une augmentation de la pente et du degré d'exposition de la zone littorale. Par ailleurs, il y avait une corrélation entre la richesse en espèces et la longueur effective de l'aire de formation des vagues, mais cette corrélation n'était pas linéaire. Nous proposons quelques méthodes permettant d'augmenter la précision des modèles servant à estimer la production de poissons dans les habitats littoraux. Les mesures de conservation devraient viser à protéger non seulement les habitats littoraux pourvus de végétation et productifs, mais également les zones voisines qui profitent elles aussi de cette forte productivité.
[Traduit par la Rédaction]

Introduction

Submerged macrophytes in the littoral zone of lakes provide an important habitat for fishes. Macrophytes provide a reproductive environment for phytophilic fish species, they provide structure and cover for protection from predators, and by harbouring a rich invertebrate fauna, macrophytes provide a productive feeding environment. Relationships between macrophytes and fish depend on geographic area, plant species composition and form, type of aquatic system (lotic vs. lentic), and composition of the fish community (Killgore et al. 1993). Generally, macrophytes are expected to increase nearshore productivity (Jude and Pappas 1992). However, quantitative evidence of the relation between macrophytes and other habitat features and fish production in littoral habitats is limited.

This study links fish abundance with the density of submerged macrophytes in littoral habitats of the Great Lakes. Specifically, we test for the relationships between macrophyte density and fish species richness and fish size, density, and biomass. Fish production is not measured directly, but a production index is estimated from measures of biomass and fish size. In addition, we test if the production index can be predicted from information on macrophyte density and other

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habitat features, including slope of the littoral area, wind exposure, effective fetch, substrate composition, and phosphorus concentration. Littoral areas of the Great Lakes are of special interest because of their linkages with the large pelagic offshore areas, which interact with and influence the inshore areas both physically and biologically.

Methods

Data sources

Fish

Electrofishing surveys, using a 6.1-m boat, were conducted in 1990 at five areas: Hamilton Harbour and Bay of Quinte in Lake Ontario and three bays of Severn Sound (Penetang, Hog, and Matchedash bays), which are located in southeastern Georgian Bay, Lake Huron. Electrofishing was conducted at 1.5 m depth, along 100-m transects. Transects were sampled monthly from June to August. Because we wanted to test for fish–vegetation associations, only August samples, when macrophytes were well established, were included. The number of transects by area were Hamilton, 20; Quinte, 20; Penetang, 29; Hog, 14; Matchedash, 12. We sampled 95 separate transects in total. Information on species richness (SR; number of species per transect), fish size (W; weight in grams), fish numbers (D; number per transect), and biomass (B; total grams of fish per transect) was recorded. Electrofishing procedures and transect locations are described by Randall et al. (1993).

Macrophytes

Macrophyte density was estimated at a subset (68) of the transects in late August or early September, 1990. Macrophyte density was estimated by visual observation of percent cover, and by diving surveys to determine stem density (Minns et al. 1993). Percent macrophtye cover was a function of stem density and plant height (Minns et al. 1993), and percent cover was a useful variable for predicting fish species associations (Minns et al. 1994). Percent cover was used as a continuous variable (COVER, transformed using square root arc sine) or as a categorical variable (VEG). Transects were assigned to one of four vegetation categories: absent (0% macrophyte cover, $n = 7$ transects), sparse (1–30%, $n = 30$), moderate (31–70%, $n = 7$), and heavy (70%, $n = 24$).

Physical features

Littoral slope (SLOPE) was calculated as 1.5 m/min. × 1000, where min. was the minimum distance in kilometres from the transect to the shore. Maximum wind exposure (MAX) was the maximum overwater distance from the transect to a shoreline. Effective fetch was based on the prevailing wind direction. Effective fetch (FETCH, kilometres) was calculated for angles –45° to 45° at 22.5° intervals relative to the prevailing wind direction using a formula provided by Scheffer et al. (1992): FETCH = sum(cos(ang) × F(ang))/sum(cos(ang)), where ang is the angle to prevailing wind and F is the distance along direction in kilometers. A prevailing wind direction of southwest was used for all areas (Saulesleja 1986). For distance measurements, transect locations were marked on Ontario Base Maps (Hamilton), hydrographic charts (Severn Sound), or topographic maps (Quinte). Shorelines and transects were digitized. Distances from transects to shore were measured for 16 compass points (i.e., 22.5° intervals).

Substrate was sampled at 6 locations on 26 transects (beginning and end of transects, and at points 5 m inshore and 5 m offshore at each end of the transect) using an Ekman dredge for fine sediments, or by visual observation. Substrate was classified as: silt (<0.063 mm), sand (≥0.063 but <2 mm), gravel (≥2 but <16 mm), and rock (>16 mm). Substrates were converted to a Phi scale (PHI) according to Hakanson and Jansson (1983) as follows: silt = 6.5, sand = 2, gravel = –3.5, and rock = –6.0. The first and last Phi categories were approximations; silt included coarse to fine silt, clay, and mud and rock included all substrates from coarse gravel to boulders.

Total phosphorus concentrations (PHOS) were available for four of the five bays, but only at eight different locations (three in Bay of Quinte, three in Penetang, and one each in Hamilton and Hog bays; Randall et al. 1993). Individual survey transects were assigned a value based on the phosphorus record from the closest location. Phosphorus concentrations for Matchedash Bay were assumed to be the same as Hog Bay (Randall et al. 1993), which is located to the west of Matchedash Bay.

Production index

Boudreau and Dickie (1989) developed a multiple regression equation to predict population fish production (P): $\log_{10} P = \log_{10} a + b \log_{10} W + c \log_{10} B$, where W is mean fish size at maturity, and B is average annual biomass. For whole fish communities, coefficients b and c were determined empirically to be –0.35 and 0.90, respectively, by Randall et al. (1995). Biomass is the dominant independent variable in the regression, but production is also adjusted for average fish size. The coefficient a is a scaling factor which depends on habitat features. Using the Boudreau and Dickie equation as a base, a production index (PI) was calculated for each transect as: $\log_{10}$ PI = $-0.35\log_{10} B + 0.90\log B$. Because our estimate of B was not a seasonal average, and because sampling efficiency was unknown, the index provided a relative index of production only. Differences in production between habitats (e.g., vegetated versus unvegetated areas) can be inferred using PI if the observed differences in biomass and mean fish size between habitats are consistent over time.

Biomass, the second regressor in the above equation, is the product of mean fish size (W) and fish numbers (D). Fish abundance and mean fish size are not independent, but are negatively correlated (Randall et al. 1995). Bohlin et al. (1994) used a linear plot of log D versus log W, to make inferences about differences in habitat productivity. We plotted community fish abundance versus mean fish size, and compared the data from vegetated and unvegetated sites.

Statistical analyses

Four steps were involved in the statistical analyses. (*i*) Differences in fish species richness, numbers, and fish weight among the four vegetation categories were tested using unbalanced ANOVA and Scheffe's test. (*ii*) To examine relationships between fish measures (numbers, biomass, size, production index, and richness) and the habitat features (% cover, exposure, fetch, slope, substrate, and phosphorus), correlation matrices (Pearson) were examined. Fish and habitat measures are listed in Table 1. Probabilities associated with the correlations were first adjusted for multiple comparisons (Bonferroni adjustments). Scatterplots were also examined to detect nonlinear relationships between variables. LOWESS, a weighted smoothing procedure that, unlike linear or quadratic smoothing, does not presuppose the shape of the function (SYSTAT Inc. 1992), was used for the scatterplots. (*iii*) Next, the relationship between fish numbers and fish size was examined by plotting $\log_{10} D$ against $\log_{10} W$. Analysis of covariance, with a dummy variable for vegetation, was used to test for the effect of macrophytes on the fish number – fish size relationship. (*iv*) Finally, the relationship between the fish measures (species richness, biomass, etc.) and habitat features was examined collectively using stepwise multiple regression analysis. Minimum tolerance to enter into the model was 0.01, and alpha-to-enter and alpha-to-remove levels of 0.15 were used. Frequency plots of fetch, slope and exposure were skewed, so these variables were transformed (log base 10) for the regression analysis.

Fish species assemblage was different at Hamilton Harbour than at other areas (Minns et al. 1994; Randall et al. 1993). For this reason, a dummy variable (DUM) was added for Hamilton (Hamilton = 1, other areas = 0) in the regression analyses.

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Table 1. Summary of fish and habitat data collected from littoral habitats at three areas of the Great Lakes (Hamilton Harbour, Bay of Quinte, and Severn Sound).

Data type	Measure	*N*	Mean	Range	SE	CV
Fish	Species richness (SR)	68	5.1	0–12	0.39	0.63
	Numbers (*D*)	68	50.0	0–276	7.11	1.17
	Weight (*W*, g)	66	381.0	9–3940	93.45	1.99
	Biomass (*B*, g)	68	5174.4	0–30 137	684.63	1.09
Macrophytes	Percent cover	68	42.2	0–100		
	Density (no.·m^{-2})[a]	72	448.1	0–7127		1.07
Physical	Maximum exposure (km)	68	4.72	0.52–20.15	0.45	0.79
	Littoral slope	67	0.05	0.004–0.632	0.01	1.62
	Effective fetch (km)	68	0.941	0.010–3.483	0.122	1.07
	Substrate (PHI units)	26		−6.0–6.5		
	Phosphorus (μg·L^{-1})			15.6–49.0		

Note: Field methods used to collect the fish and habitat measures are described in the text.
[a]From Minns et al. 1993.

Results

Variability in the habitat measures

Percent bottom cover by submerged macrophytes varied from 0 to 100%, with an average of 42% (Table 1). Mean percent cover was less at Bay of Quinte (22%) and Hamilton Harbour (11%) than at Severn Sound (66–76%). The dominant plant genera were *Vallisnera*, *Myriophyllum*, *Potamogeton*, and *Elodea*, but relative abundance and composition varied among areas (Minns et al. 1993).

Percent cover was significantly but negatively correlated with phosphorus and maximum exposure ($P < 0.001$), and positively correlated with substrate, as measured by the Phi index ($P < 0.01$). High percent cover was associated with fine sediments. Multiple regression analysis indicated that percent cover was significantly related to three habitat variables: effective fetch, phosphorus, and maximum exposure ($F = 15.01$; df = 3, 64; $R^2 = 0.39$; $P < 0.001$). Using the smaller sample of transects for which substrate was known, percent cover was related to substrate, but fetch, exposure, and phosphorus did not remain in the stepwise regression ($F = 8.46$; df = 1, 24; $R^2 = 0.23$; $P < 0.01$).

The range and average of the physical habitat measures, including littoral slope, exposure, effective fetch, phosphorus, and substrate, are summarized in Table 1. Effective fetch and littoral slope were negatively correlated ($P < 0.001$). Substrate (Phi index) was also negatively correlated with maximum exposure ($P < 0.01$).

Species richness

A total of 31 species of fish were captured at the 95 transects. The percent frequency of occurrence by species is shown for each study area in Table 2. Species richness varied from 0 to 12 among transects, with a mean of 5.1 (Table 1). Richness varied significantly among the four macrophyte categories (ANOVA, $F = 10.38$, $P < 0.001$), ranging from a low average of 2.4 (macrophytes absent) to 7.4 (macrophyte density moderate) (Fig. 1*a*). Species richness was significantly lower where macrophytes were absent or sparse than where macrophytes were moderate or heavy.

Fish species richness was also significantly but negatively correlated with slope (Fig. 2*a*) and exposure. Scatterplots indicated that the relationship between richness and effective fetch was not linear (Fig. 3*a*).

The multiple regression between species richness and habitat features with the highest coefficient of determination included cover, littoral slope, fetch (as a quadratic), and DUM (Table 3, regression 1). DUM was a dummy variable for Hamilton Harbour and indicated species richness was significantly less in Hamilton than at the other areas.

Fish numbers

The number of fish captured varied from 0 to 276 fish per transect, with a mean of 50 (Table 1). Catches varied significantly among the four macrophyte categories ($F = 9.82$, $P < 0.001$). Density of fish in the high macrophyte category was significantly greater than in the absent and sparse categories (Fig. 1*b*). As with species richness, the results indicated that classification of macrophyte cover into two categories (high and low) was adequate.

Fish abundance was negatively correlated with average fish size (Fig. 4). Transects where only one fish was captured ($n = 4$) were outliers in this regression and were removed (Studentized residual >3.0). The coefficient of determination was 0.45 (Table 3, regression 2). Analysis of covariance, with VEG entered as a dummy variable (VEG <50% = 0, VEG >50% = 1), indicated that fish numbers were significantly higher at vegetated transects, after adjustment for fish size. Slopes of the regressions were not different between the high and low macrophyte density sites ($F = 1.61$, df = 1, 58, $P = 0.21$). Adjusted for the covariate, fish abundance was 2.3 times higher at high macrophyte density sites than at low macrophyte density sites.

Fish catches were negatively correlated to littoral slope (Fig. 2*b*) and exposure. As with species richness, the relationship between fish density and effective fetch was apparently not linear (Fig. 3*b*). The multiple regression for predicting fish abundance included fish size, percent cover, species richness, phosphorus, and littoral slope as independent variables (Table 3, regression 3). When species richness was removed from the model, cover, slope, and exposure remained significant, but the coefficient of determination was lower ($R^2 = 0.48$ versus 0.77; Table 3).

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Table 2. List of the 31 species of fish captured at the 95 survey transects.

Species	No.	Percent frequency				
		Hamilton	Quinte	Penetang	Hog	Matchedash
Perca flavescens	2643	5.0	90.0	82.8	85.7	83.3
Alosa pseudoharengus	730	50.0	20.0	27.6	14.3	58.3
Lepomis gibbosus	676	20.0	65.0	65.5	92.9	75.0
Dorosoma cepedianum	219	15.0	35.0	0.0	0.0	41.7
Pimephales notatus	209	0.0	0.0	27.6	21.4	0.0
Ameiurus nebulosus	207	40.0	25.0	17.2	0.0	58.3
Catostomus commersoni	163	0.0	20.0	58.6	14.3	75.0
Pomoxis nigromaculatus	157	0.0	15.0	27.6	50.0	83.3
Micropterus salmoides	146	5.0	45.0	71.7	71.4	66.7
Ambloplites rupestris	82	0.0	50.0	27.6	21.4	58.3
Morone americana	81	10.0	45.0	0.0	0.0	0.0
Notemigonus crysoleucas	73	0.0	40.0	10.3	21.4	58.3
Notropis heterodon	52	0.0	0.0	27.6	35.7	0.0
Cyprinus carpio	50	55.0	40.0	20.7	14.3	16.7
Percina caprodes	40	0.0	45.0	0.0	0.0	16.7
Notropis atherinoides	40	10.0	35.0	13.8	0.0	0.0
Stizostedion vitreum	36	0.0	45.0	0.0	0.0	16.7
Lepomis macrochirus	29	0.0	35.0	0.0	0.0	0.0
Micropterus dolomieu	26	5.0	20.0	31.0	0.0	0.0
Esox lucius	21	5.0	45.0	6.9	7.1	8.3
Notropis hudsonius	17	5.0	60.0	0.0	0.0	16.7
Carpiodes cyprinus	15	0.0	0.0	27.6	0.0	8.3
Aplodinotus grunniens	14	10.0	30.0	0.0	0.0	0.0
Labidesthes sicculus	11	0.0	30.0	3.4	7.1	0.0
Amia calva	6	0.0	10.0	0.0	0.0	25.0
Moxostoma macrolepidotum	2	0.0	10.0	0.0	0.0	0.0
Carassius auratus	2	10.0	0.0	0.0	0.0	0.0
Umbra limi	1	0.0	5.0	0.0	0.0	0.0
Fundulus diaphanus	1	0.0	0.0	3.4	0.0	0.0
Etheostoma nigrum	1	0.0	5.0	0.0	0.0	0.0
Morone chrysops	1	5.0	0.0	0.0	0.0	0.0
No. of transects	—	20	20	29	14	12

Note: The percent frequency of occurrence of each species (percentage of transects where the species occurred) is shown by study area.

Fish size

Average fish size per transect varied from 9 to 3940 g, with a mean of 381 (Table 1). Mean fish size was related to macrophyte density ($F = 5.00$, $P = 0.004$) (Fig. 1*c*), but variability in fish size within the macrophyte categories was high. Fish weight was significantly different between the heavy and sparse macrophyte categories only (Scheffe test, $P = 0.005$).

Fish size was also correlated with maximum exposure and phosphorus ($P < 0.05$) and to slope (Fig. 2*c*). Fish size was related to fetch in a nonlinear manner (Fig. 3*c*). The multiple regression relating fish size to habitat features included phosphorus, slope, and exposure as significant independent regressors, but not percent cover (Table 3, regression 5).

Biomass

Biomass per transect varied from 0 to 30 137 g (Table 1). Biomass did not differ significantly among the macrophyte categories ($P = 0.30$).

Examination of the correlation matrix indicated that biomass was only weakly associated with habitat features: only phosphorus was significantly correlated with biomass ($P < 0.043$). The stepwise regression analysis with biomass as the dependent variable indicated that species richness and phosphorus were significant regressors (Table 3, regression 6). When habitat variables only were used in the stepwise procedure, phosphorus, slope, and cover were significant regressors with biomass, but explained only 36% of the variance (Table 3, regression 7).

Production index

The production index differed significantly among the macrophyte categories. Mean $\log_{10}$ PI in each of the VEG categories was absent, 2.04; sparse, 2.24; medium, 2.59; and heavy, 2.57 (ANOVA, $P < 0.009$). When only two macrophyte categories were used, the production index was 2.5 times higher at transects where cover was greater than 50% than at transects where cover was less than 50% ($P < 0.001$).

The production index was positively correlated with cover and species richness, and negatively correlated with littoral slope ($P < 0.05$). Stepwise multiple regression indicated that cover, richness, and phosphorus best predicted the production index ($R^2 = 0.61$; Table 3, regression 8). The regression that included only habitat features, percent cover, phosphorus, and

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Fig. 1. Comparison of species richness (*a*), number (*b*), and average weight (*c*) of fish captured at sites with varying densities of macrophytes. Macrophyte densities were: absent, 0% cover (n = 7); sparse, 1–30% (n = 30); medium, 31–70% (n = 7); heavy, 70% (n = 24). Error bars indicate 1 SE.

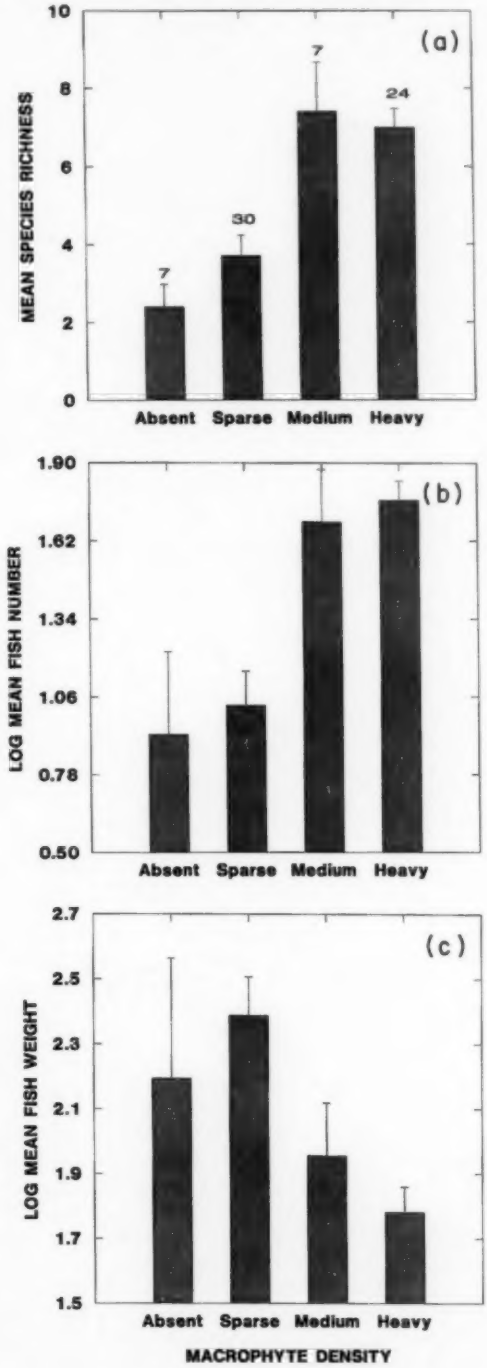

Fig. 2. Scatterplots to show the relationship between littoral slope and fish species richness (*a*), fish number (*b*), and average fish weight (*c*) at the survey transects. Trend lines were calculated using weighted sequential smoothing (LOWESS procedure of SYSTAT Inc. 1992).

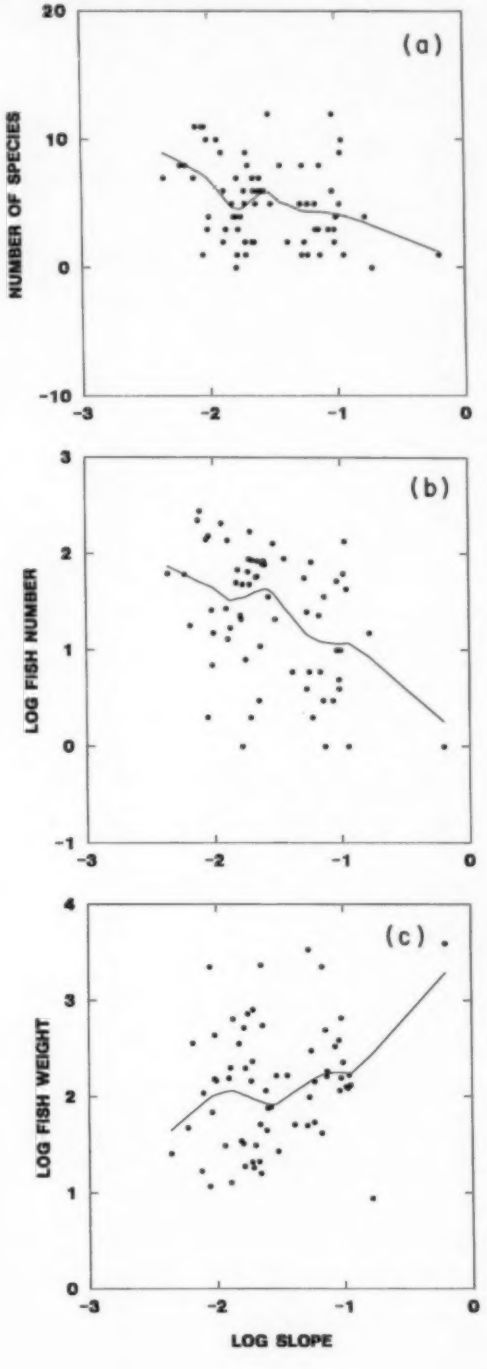

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Fig. 3. Scatterplots to show the relationship between effective fetch and fish species richness (*a*), number (*b*), and average weight (*c*) of fish at the transects. Effective fetch (distance in km) was calculated for prevailing wind direction (see text) Trend lines were calculated using weighted sequential smoothing (LOWESS procedure of SYSTAT Inc. 1992).

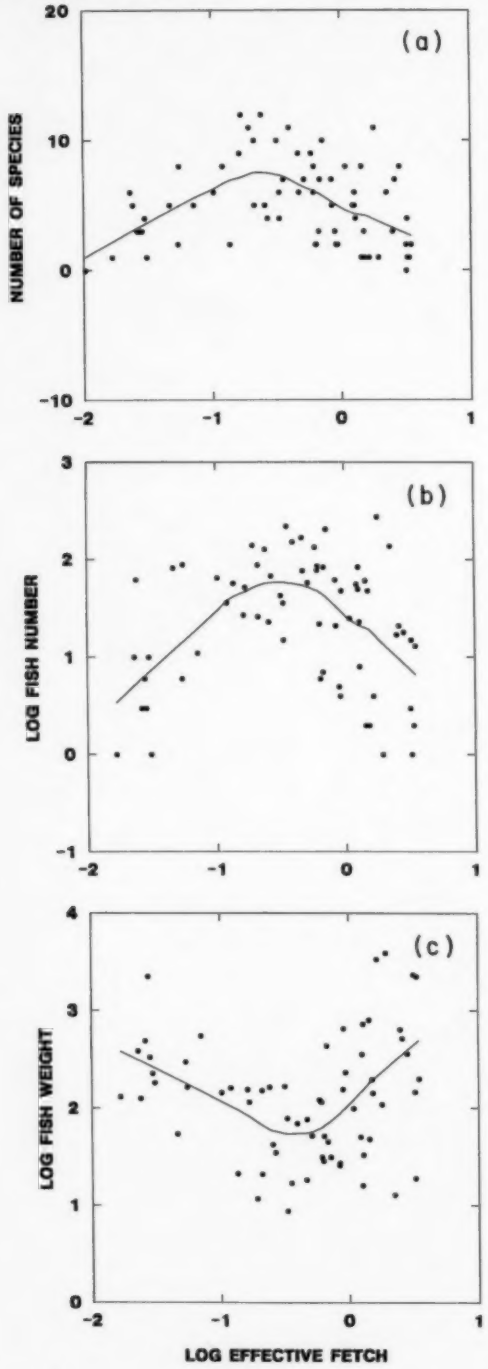
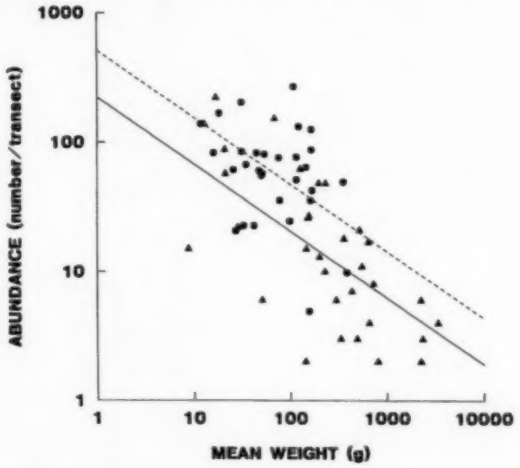


Fig. 4. Relationship between fish abundance (*D*; number of fish captured per transect) and fish weight (*W*; mean fish weight at transect in grams) for samples collected by electrofishing at 66 different transects in littoral areas of Hamilton Harbour, Bay of Quinte, and Severn Sound. Transects at heavily vegetated sites (% cover >50%) are indicated with circles and sites where vegetation was low or absent are indicated with triangles. Slopes were not different, but intercepts were significantly different between the two vegetation categories. The regression equation was: $\log_{10} D = 2.346 - 0.516 \log_{10} W + 0.36$ DUM ($R^2 = 0.52$), where DUM is a dummy variable for the vegetation categories of low (DUM = 0) and high (DUM = 1). Note that in addition to the different intercepts, fish size at transects with low macrophyte density was greater than at transects with high macrophyte density.



slope had a lower coefficient of determination ($R^2 = 0.43$; Table 3, regression 9).

Discussion

Production index and macrophytes

The production index calculated from fish samples collected in August was significantly higher in vegetated areas than in adjacent areas with low densities of submerged macrophytes. Species diversity and density of aquatic invertebrates is high in macrophyte areas (e.g., Mills et al. 1981; Cyr and Downing 1988) and fish utilize the invertebrates as prey. In addition, macrophytes increase the structural complexity of the littoral habitats, which increases fish species richness and influences predator–prey interactions (Crowder and Cooper 1982; Eadie and Keast 1984). Both resource availability and predator risk influence habitat use by fishes in the littoral zone. In an inland lake, Keast and Harker (1977) found that fish biomass was concentrated in littoral areas, and the highest species richness and biomass was found in vegetated habitats (Keast et al. 1978). Few estimates of fish production have been made in littoral areas, particularly in the Great Lakes (Edwards et al. 1989; Jude and Pappas 1992). Our results indicate that the fish production index, based on measures of fish abundance and fish size, was significantly higher at littoral sites with macro-

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Table 3. Summary of statistics for regression models that link fish density (*D*), fish size (*W*), species richness (SR), biomass (*B*), and production index (PI) with habitat features.

Regression	Dependent	Independent	Coefficient	Probability	R^2	*N*
1	SR	constant	0.88	0.58	0.47	67
		COVER	1.68	0.01		
		log FETCH	–2.92	0.01		
		log $FETCH^{-2}$	–2.00	0.01		
		log SLOPE	–2.38	<0.01		
		DUM	–1.50	0.06		
2	log D	constant	2.78	<0.01	0.45	62
		log W	–0.64	<0.01		
3	log D	constant	0.38	0.35	0.77	62
		log W	–0.52	<0.01		
		COVER	0.20	0.02		
		log PHOS	0.84	<0.01		
		log SLOPE	–0.19	0.04		
		SR	0.09	<0.01		
4	log D	constant	0.07	0.79	0.48	65
		COVER	0.48	<0.01		
		log MAX	–0.51	0.01		
		log SLOPE	–0.80	<0.01		
5	log W	constant	0.95	0.05	0.35	65
		log PHOS	1.19	<0.01		
		log SLOPE	0.58	<0.01		
		log MAX	0.59	<0.01		
6	log B	constant	1.05	0.01	0.46	65
		SR	0.09	<0.01		
		log PHOS	1.35	<0.01		
7	log B	constant	0.52	0.29	0.36	64
		COVER	0.37	<0.01		
		log PHOS	1.61	<0.01		
		log SLOPE	–0.25	0.05		
8	log PI	constant	0.38	0.22	0.61	65
		COVER	0.15	0.06		
		SR	0.09	<0.01		
		log PHOS	0.97	<0.01		
9	log PI	constant	–0.04	0.92	0.43	64
		COVER	0.44	<0.01		
		log PHOS	1.07	<0.01		
		log SLOPE	–0.38	<0.01		

Note: Habitat measures are COVER, percent cover (square root arc sine); PHOS, total phosphorus; SLOPE, slope from shore to 1.5-m depth contour; FETCH, effective fetch; MAX, maximum exposure (see text).

phyte beds than at sites where macrophytes were sparse or absent.

Examination of the fish abundance – fish size plot provided the first evidence that fish abundance was related to macrophyte density. Slopes of the regressions for the high and low macrophyte density habitats were not different, but the intercept for the high macrophyte sites was higher than for the low macrophyte sites, indicating that density of fish was higher in the former habitats after adjustment for fish size. Also, fish size was consistently smaller at the high macrophyte sites. Both of these factors are consistent with the hypothesis that production was higher where macrophytes were abundant. Barnett and Schneider (1974) also observed that as plant density increased, greater numbers of smaller fish were found. The production index, which was based on both biomass and fish size, was over two times higher in the dense macrophyte areas than at sites where macrophytes were scarce or absent.

Bohlin et al. (1994) and Randall et al. (1995) found that the slope of fish density versus fish size regression was not significantly different from –0.9 for stream salmonids, and for community measures of fish production, respectively. The slope in this study was significantly less (–0.64; $F = 8.4$, df = 1, 60, $P < 0.005$), and may have resulted from the size-dependent catchability of fish. Electrofishing gear is known to be selective,

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Table 4. Summary of habitat features that were significantly correlated with fish species richness (number of species per transect), numbers (number of fish captured per transect), mean fish weight per transect, biomass (total weight at transect), and the production index (see text).

	Species richness (SR)	Density (*D*)	Weight (*W*)	Biomass (*B*)	Production index (PI)
Percent macrophyte cover	+	+	–	+	+
Phosphorus		+	+	+	+
Littoral slope	–	–	+	–	–
Maximum exposure	–	–	+		
Effective fetch	Quadratic	Quadratic	Quadratic		

Note: Significance was determined by Pearson correlation or by stepwise multiple regression (see text). Relationships are indicated as being positive, negative, or quadratic (nonlinear).

with smaller fish being less vulnerable to electric shock than larger fish (Zalewski and Cowx 1990). The presence of vegetation may also hide fish fleeing from the electrical current, and contribute to a lower catchability. Reduced catch efficiency of smaller fish would reduce the slope of the fish density – fish size plot. Reduced catch efficiency would also lead to biased catches across habitats: fish abundance (and hence the production index) at the vegetated transects may have been underestimated.

Among the macrophyte density categories, significant differences were found in fish numbers, size, and the production index, but not in biomass. Biomass is the product of mean size and density, and because these two variables were inversely correlated, overall biomass tended to vary less than either of the two components. Because the production index accounts for the influence of fish size and biomass, it may be a more sensitive measure than biomass alone. The analysis now needs to be applied to data collected seasonally. Our objective was to demonstrate the potential utility of the method, and to identify, however roughly, the magnitude of the difference in production index between vegetated and unvegetated littoral habitats. The density–fish size relationship and the production index are potentially useful tools for interpreting differences in productivity of different habitats (Elliott 1993; Bohlin et al. 1994; Randall et al. 1995). However, the production index must be evaluated further, particularly for interpreting data at the fish community level.

Production index and other habitat features

In addition to macrophytes, other factors that were related to fish abundance, size, and the production index were phosphorus, littoral slope, exposure to wind, and effective fetch (Table 4). In whole lake ecosystems, Downing et al. (1990) and Downing and Plante (1993) showed that fish biomass and fish production were significantly and positively correlated with phosphorus concentrations, both at the population and community level. This study and Randall et al. (1993) showed that biomass was significantly correlated with phosphorus, but it was not clear whether there was a functional relationship. All our transects were contiguous with the greater lake environment. Phosphorus levels in the open lake were much lower. Is it possible to detect responses in fish biomass to these localized elevations in phosphorus? Interestingly, fish density, biomass, and the production index were all positively related to phosphorus, after adjustment for percent macrophyte cover. Phosphorus seems to be a correlate to fish density and biomass, even in localized inshore areas.

Wind exposure and effective fetch determine the amount of mechanical energy (wave action, wind driven currents, convective currents) affecting the nearshore environment. Exposed shorelines may be suboptimal for plants because of the mechanical force of wave action can cause physical damage (Wilson and Keddy 1986), because of increased turbidity, and also because exposure can influence the characteristics of the sediment. Bailey (1988) found that macrophyte species richness was inversely correlated with wind exposure in Long Point Bay, Lake Erie. Intermediate levels of exposure may be beneficial to plants. Deposition of suspended solids on the vegetation adds to the epiphyte complex, which in turn can reduce light levels at the leaf surface (Scheffer et al. 1992). Wave action can reduce the epiphyte layer and enhance photosynthesis by increasing diffusion at the plant surface (Wetzel 1992). Thus, there may be both negative and positive effects of wave action on plants. Species richness of macrophytes in inshore communities may peak at intermediate levels of exposure, at least at some locations (Keddy 1983).

In our study, slope was inversely correlated with fetch. Slope has an important effect on the physical environment because it will determine the extent and dynamic nature of the littoral habitat. Slope may influence convective circulation, which can be a significant factor in renewing littoral waters (Horsch and Stefan 1988). Mann (1988), citing Bowen (1979), noted that the slope of the littoral bottom had an effect on the composition of organic matter. Resuspension or displacement of organic matter in the littoral zone is a function of both exposure and shoreline morphometry.

Gradients in productivity in the nearshore zone will influence the distribution of fish. Densities and species richness of fish may be highest at intermediate exposed sites, because of controlling factors similar to those which influence macrophytes and the transport of detritus in the inshore areas. Fish production may be positively related to mechanical energy, such as tides, wind, and water current (Nixon 1988; Randall et al. 1995). Obviously there is an upper limit, and fish density or occurrence would be reduced at very high energy areas. The nonlinear relationship between fetch and fish density and species richness may be a response to this energy gradient, both because of indirect effects on macrophytes and detritus and also because of direct effects on fish. The spatial distribution of fish in inshore habitats is influenced by both biological and physical processes. Macrophytes and detritus provide the organic base that is utilized by the higher trophic levels, including fish, but the morphometry and exposure characteristics of littoral habitats define the dynamic physical environment, which is equally important in influencing and determining production.

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Future work

Fish production, as inferred from biomass and fish size structure, varied spatially in the littoral areas and was related to specific biological and physical habitat characteristics. Our study showed that the amount of variability that could be explained with habitat information alone was low. When both fish and habitat variables were regressed with fish density and the production index, the regression models explained 61–77% of the variability, but when habitat variables alone were used, coefficients of determination were less than 50%. At this stage, the regression models are of limited use for prediction, but they help to identify the habitat factors which are important to fish. With further refinement and confirmation, our results could be useful to habitat managers. The habitat features which were related to fish structure and abundance are measurable remotely (using hydrographic charts and aerial photos to determine slope, exposure, fetch, macrophyte density). In future, it may be possible to conduct nearshore habitat evaluations to determine habitat supply over extensive areas, possibly with minimal field work.

Future work will focus on a closer examination of the spatial effects (proximity) of habitat features on fish, at the community, guild, or individual species level. Spatial autocorrelation has only recently been considered in studies of habitat–abundance relationships in littoral fish (Hinch et al. 1994), but clearer patterns may be discernable if data are corrected for geographic influences. Indices of production, such as the production index used above, must be validated. Littoral habitats in the Great Lakes are unique because of the size and nature of the offshore areas that influence them. Our knowledge of factors that influence the productive capacity of the Great Lakes habitats must be improved if these areas are to be preserved or restored in future.

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Design and management of bird nesting habitat: tactics for conserving colonial waterbird biodiversity on artificial islands in Hamilton Harbour, Ontario

J.S. Quinn, R.D. Morris, H. Blokpoel, D.V. Weseloh, and P.J. Ewins

Abstract: Hamilton Harbour, at the west end of Lake Ontario, supports breeding colonies of six piscivorous waterbirds: double-crested cormorant (*Phalacrocorax auritus*), black-crowned night-heron (*Nycticorax nycticorax*), herring gull (*Larus argentatus*), ring-billed gull (*Larus delawarensis*), common tern (*Sterna hirundo*), and Caspian tern (*Sterna caspia*). Most breeding pairs of all species nest on privately owned mainland locations that are subject to multiple industrial and development activities. The construction of three artificial islands in the eastern basin of Hamilton Harbour in the winter of 1995–1996 presents an opportunity to simultaneously reduce current land-use conflict and maintain the existing avian biodiversity. Accordingly, we used ecological information to determine suitable substrates and vegetation to satisfy nesting habitat preferences and to facilitate the occupation of the islands by nesting waterbirds. Our recommendations for habitat design and management emphasize techniques to prevent displacement of both tern species by ring-billed gulls and of night-herons by cormorants. We propose long-term management procedures based on aspects of the biology and known ecological interactions among the various species.

Résumé : Le havre de Hamilton, situé à l'extrémité ouest du lac Ontario, héberge des colonies reproductrices de six oiseaux aquatiques piscivores : le cormoran à aigrettes (*Phalacrocorax auritus*), le bihoreau gris (*Nycticorax nycticorax*), le goéland argenté (*Larus argentatus*), le goéland à bec cerclé (*Larus delawarensis*), la sterne pierregarin (*Sterna hirundo*) et la sterne caspienne (*Sterna caspia*). Chez toutes ces espèces, la plupart des couples de reproducteurs nichent sur la terre ferme, sur des terrains privés soumis à de multiples activités industrielles ou travaux d'aménagement. La construction de trois îles artificielles dans le bassin est du havre, à l hiver 1995–1996, est une occasion d'atténuer le conflit qui touche en ce moment l'utilisation des terres et de préserver en même temps la diversité actuelle de la faune ailée. Nous avons donc utilisé les données écologiques pour déterminer quels substrats et quels types de végétation conviennent à la nidification, afin de répondre aux préférences des oiseaux aquatiques et de faciliter l'occupation des êles par ceux-ci. Nos recommandations en matière de conception et de gestion des habitats privilégient les techniques qui permettent d'éviter le déplacement des deux espèces de sternes par le goéland à bec cerclé et du bihoreau gris par le cormoran à aigrettes. Nous proposons un mécanisme de gestion à long terme fondé sur les divers aspects de la biologie des oiseaux et sur les interactions écologiques connues entre les diverses espèces.
[Traduit par la Rédaction]

Introduction

Habitat degradation by humans has reduced biodiversity at global, and often local, levels. Loss of suitable habitat appears to be the greatest threat to colonial waterbird species in North America (Parnell et al. 1988). In Hamilton Harbour, Lake Ontario (43°16′N, 79°46′W) extensive wetlands along the south shoreline have been lost to industrial development over the past 100 yr (Hamilton Harbour Remedial Action Plan (RAP) 1992[2]).

Beginning with intermittent breeding colonies in the mid-1970s (Dobos et al. 1988), Hamilton Harbour has become one of the most important colonial waterbird nesting areas in the Great Lakes basin in the 1990s (Blokpoel and Tessier 1991). Largely cut off from human and other mammalian interference by busy fenced highways, the regions locally known as Windermere Basin and piers 25, 26, and 27 (Fig. 1) have provided nesting habitat for several avian colonial species: double-crested cormorants (*Phalacrocorax auritus*), black-crowned

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night-herons (*Nycticorax nycticorax*), herring gulls (*Larus argentatus*), ring-billed gulls (*L. delawarensis*), common terns (*Sterna hirundo*), and Caspian terns (*S. caspia*).

Three of these species warrant special concern. Common terns in the Great Lakes have been declining in numbers and are listed as endangered, threatened, or of special concern by most states bordering the Great Lakes (Courtney and Blokpoel 1983; Kress et al. 1983; Blokpoel and Scharf 1991). Caspian terns have been designated as vulnerable in Canada (COSEWIC 1992), endangered in Wisconsin, and threatened in Michigan (Blokpoel and Scharf 1991). Recently, Austen et al. (1994) recommended adding the black-crowned night-heron to the list of rare species and downlisting the Caspian tern to "rare" status. The continued existence of these breeding colonies at Hamilton Harbour is in jeopardy because of development plans for the privately owned property where the birds nest. Most individuals of all of these species nest on property owned and under development by the Hamilton Harbour Commissioners.

The Fish and Wildlife Restoration Project of the Hamilton Harbour RAP has implemented the construction of three wildlife islands in northeastern Hamilton Harbour (Hamilton Harbour RAP 1992; see footnote 2), expected to begin in the winter of 1994–1995 (Fig. 1). The islands are designed to accomplish multiple goals, principal among them: (*i*) to break wave action to reduce turbidity in the lee of the islands (thus allowing submerged vegetation growth and increases in associated fish populations) and (*ii*) to provide protected habitat for amphibians, reptiles, and especially colonially nesting waterbirds (Hall 1991[3]). Construction of these islands provides a valuable opportunity to simultaneously reduce land-use conflicts and protect and manage the local waterbird biodiversity.

We propose a management plan for creating habitat on artificial islands and managing colonially nesting waterbirds with two distinct though compatible goals. First, we seek to maintain and monitor the local biodiversity of colonial waterbirds in Hamilton Harbour. Second, we focus special efforts on the two tern species and the black-crowned night-heron to conserve these colonial species in the Great Lakes. These goals can be accomplished by creating nesting habitat and by managing the colonies on the islands, including control of ring-billed gulls, double-crested cormorants, vegetation, and human disturbance.

Below we describe the ecological characteristics of each of the major colonial waterbird species that nest at Hamilton Harbour. We then discuss the resulting conservation issues, final design features for the newly created habitat, and the short- and long-term management plans for the area. Some of the proposed approaches are without precedent and require further evaluation.

Species accounts

Double-crested cormorant

Nesting chronology and nest site

Double-crested cormorants nesting in Ontario begin laying eggs in the latter part of April. Because of their inaccessible nests in spindly trees at Hamilton Harbour, data on clutch initiation are lacking. Peck and James (1983) list 27 April – 30 August as dates when eggs are present in nests, with most (50%) of the records occurring between 5 June and 5 July. Data from eastern Lake Ontario suggests somewhat earlier clutch initiation. At Pigeon and Little Galloo Islands in Lake Ontario, clutch initiation was well advanced by the third week of April with 16–35% of the nests present having eggs at Pigeon (1990–1992; D.V. Weseloh, unpublished data), and 5–10% having eggs at Little Galloo (1985–1986; Weseloh and Ewins 1994). For management purposes, one may expect cormorant eggs in nests at Hamilton Harbour by the third or fourth week of April.

Great Lakes cormorants nest on the ground or in trees. Tree-nesting cormorants build their nests in open and highly visible sites. Colonies typically initiated nesting in trees, often moving to the ground when tree-nesting space became limiting because of overcrowding or loss of trees (Wesoloh and Ewins 1994). Although trees appear to be preferred nesting sites (Blokpoel and Scharf 1991), tree death and subsequent toppling frequently occurs most likely resulting from the effects of cormorant guano. Pairs of cormorants that nest on the ground in the lower Great Lakes seem to prefer elevated sites such as rock piles, raised beaches, or toppled trees. The first cormorant nest in Hamilton Harbour was found on the ground in 1984 (Dobos et al. 1988). Thereafter, cormorants nested exclusively in mature cottonwood trees (*Populus deltoides*) along the western shore of the northernmost confined disposal facility until 1991 when nesting began in a box elder tree (*Acer negundo*) on Farr Island (Fig. 1; Moore et al. 1995). In 1992, some cormorant pairs nested on the ground in the vicinity of the cottonwoods.

Demography

Numbers of pairs have increased steadily since 1984; in 1993 the colony totalled 685 nests (Moore et al. 1995) making this colony the fourth largest of 13 colonies in Lake Ontario in the early 1990s (D.V. Weseloh, personal observations). Numbers of nesting pairs have increased throughout the Great Lakes at an average rate of 29% per annum since the early 1970s (Weseloh et al. 1995). This increase is likely due to several factors including reductions of DDE levels in the food source, reduced human persecution, and increased prey abundance in breeding and wintering areas (Price and Weseloh 1986; Blokpoel and Scharf 1991; Weseloh and Ewins 1994; Weseloh et al. 1995).

Interactions with other species

The acidic faeces produced by double-crested cormorants kills vegetation beneath their nests. Also, cormorants strip leaves and small branches for nesting material. As a result of this, nesting trees die and eventually become unable to support cormorant nests (Weseloh and Ewins 1994). The destruction of forest understorey cover by cormorants has necessitated culling of cormorants on some islands in the St. Lawrence River that support an eider-down industry (Bédard and Nadeau 1995). We anticipate that the guano-induced destruction of

[3] Hall, J. 1991. Fish and wildlife habitat restoration in Hamilton Harbour and Cootes Paradise, concept summary. Fish and Wildlife Restoration Committee for Hamilton Harbour and Cootes Paradise. Available from Library, Canadian Centre for Inland Waters, Box 5050, 867 Lakeshore Drive, Burlington, ON L7R 4A6, Canada.

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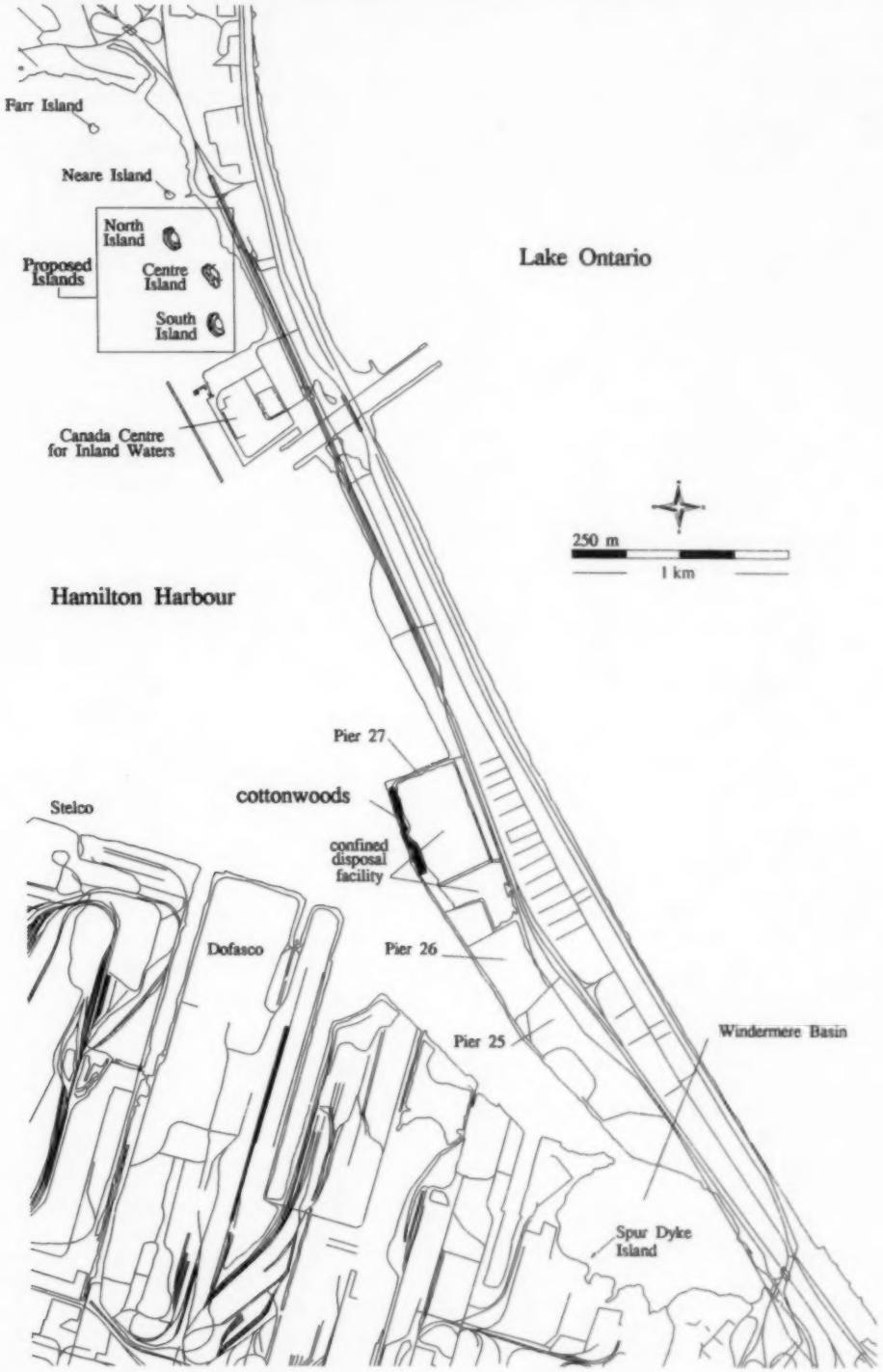
Fig. 1. Map of eastern Hamilton Harbour showing the location of current nesting colonies and proposed artificial wildlife islands. Produced under licence with the Ontario Ministry of Natural Resources.



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Carolinian forest cover and ground vegetation on some islands in the western basin of Lake Erie will soon become a considerable concern (D.V.Weseloh and P.J. Ewins, personal observations).

Ground-nesting cormorants are able to take over active nests of other colonial species, including herring gulls (P.J. Ewins, personal observations), and may take up nesting space that would otherwise be used by other ground-nesting species. Deterioration of the shrub layer by cormorants nesting overhead would reduce nesting opportunities for black-crowned night-herons.

Black-crowned night-herons

Nesting chronology and nest site

Data are lacking for Hamilton Harbour. Peck and James (1983) give 6 May – 9 September as a range of dates when eggs can be found in night-heron nests and 1–17 June as when most records occur. Field data from the Lake Ontario – Niagara River shoreline suggest somewhat earlier dates. In the Niagara River during 1991–1993, more than 80% of black-crowned night-heron nests had eggs on 26 April, although this colony may be unusually early (D.V. Weseloh, unpublished data). Night-herons that nest on Snake Island in Lake Ontario had initiated clutches by 24 April each year of 1990–1992. At Hamilton Harbour, we expect night-herons to start laying eggs by the last week of April.

Colonies are generally located in areas that are relatively inaccessible to terrestrial predators such as islands, swamps, or over open water (Davis 1993). Nests typically are built in trees or shrubs of a variety of species (Davis 1993), and a preference for concealed sites has been reported (Palmer 1962). Black-crowned night-herons nested in Hamilton Harbour in the middle branches of cottonwood trees at Pier 27; however, since 1988 they have shifted nesting to sandbar willow (*Salix exigua*) thickets along the west dyke of the confined disposal facilities. Additionally, night-herons have begun nesting in cottonwood trees along the mainland shore adjacent to Neare Island and in the box elder tree on Farr Island (Moore et al. 1995). By 1994, night-herons had begun to nest on the ground among rocks on Neare and Farr islands.

Demography

Black-crowned night-herons were first reported nesting in Hamilton Harbour in a colony of over 100 pairs during the 1950s (Dobos et al. 1988). Fifteen pairs were reported in 1959 and nests were periodically reported thereafter until 1980. Night-herons were first recorded at their current nesting site (Pier 27; Fig. 1) in 1975, numbering six pairs (Dobos et al. 1988). The population grew steadily until it reached 212 pairs in 1987 and then declined somewhat to 134 and 90 pairs in 1993 and 1994, respectively (Moore et al. 1995). This decline was coincident with an increase in the number of double-crested cormorants nesting in the cottonwoods and with a shift in nesting trees from cottonwoods to sandbar willows by the black-crowned night-herons (Moore et al. 1995). In Southern Ontario, this species is expanding its range following population declines during the late 1960s and early 1970s (Goodwin 1987); however, there are strong indications of marked declines since the 1980s in the lower Great Lakes (P.J. Ewins, unpublished data). Peck and James (1983) report a total of 8340 nests in 68 colonies across Ontario.

Interactions with other species

Black-crowned night-herons may be excluded from nesting trees by double-crested cormorants, either by direct competition for suitable branches on which to build the nests, or by defoliation of shrub layers from cormorant guano (P.J. Ewins, personal observations). Increases in numbers of cormorants nesting in Hamilton Harbour during 1988 coincided with a shift in night-heron nesting locations from the cottonwood trees, that were increasingly occupied by cormorants, to nearby sandbar willows (Moore et al. 1995). The direct causes of this shift are unknown; however, cormorant-induced defoliation of the cottonwood trees may have diminished their value as night-herons appear to prefer well-concealed nest sites (H. Blokpoel, personal observations). Additionally, cormorants may have taken over nest sites lower in the cottonwoods, forcing the night-herons out. Ring-billed and herring gulls are known to predate black-crowned night-heron eggs (Wolford and Boag 1971; P.J. Ewins, personal observations). Black-crowned night-herons are known to predate pipping common tern eggs and recent hatchlings (Hunter and Morris 1976) and immatures were observed depredating common tern nestlings in Windermere Basin during 1993 (D. Moore, personal communication). Shealer and Kress (1991) reported adult nocturnal abandonment by common terns in a colony that was disturbed by black-crowned night-herons. The combination of predation by the night-herons and the nocturnal desertion of adult terns leaving the nests vulnerable resulted in reduced tern fledging success.

Herring gulls

Nesting chronology and nest sites

Herring gulls begin nesting as early as 14 April (Peck and James 1983). In Hamilton Harbour, up to 14% of nests present had eggs by 12 and 14 April in 1989 and 1986, respectively. By 20–27 April in 1981 and 1987, up to 30% had eggs present. Peck and James (1983) also give 14 April as the earliest date on which eggs have been found in herring gull nests. Hence, we expect herring gull eggs around mid-April.

Herring gulls in the Great Lakes normally nest on islands, though some mainland nesting occurs. Nests are built on rock surfaces, including cliffs, with or without vegetation, sometimes on sand and gravel, and in grassy and weedy areas (Peck and James 1983). Additionally some nest on trees, buildings, and other human-made structures. Nests are usually slight to bulky raised mounds or platforms with variable cups, often with large bases (Peck and James 1983). Locally, herring gulls nest along the central and northern dykes of the confined disposal facilities and along the western part of Pier 27. A number of pairs began nesting on Farr and Neare islands in 1988 and 1989, respectively (Moore et al. 1995). Some isolated pairs nest among the ring-billed gulls on Pier 26, in the Windermere Basin, and on the Stelco property occasionally (Fig. 1).

Demography

Herring gulls were first reported nesting in Hamilton Harbour in 1976 when seven nests were recorded (Dobos et al. 1988). About 300 pairs have nested there each year since 1989

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(Moore et al. 1995), which represents about 5% of the lower Great Lakes population (Blokpoel and Tessier 1991).

Interactions with other species

Herring gulls sometimes act as predators on a number of other colonial ground nesters including adult and fledgling ring-billed gulls (K.M. Brown and J.S. Quinn, personal observations) and common tern adults (R.D. Morris, personal observations) and chicks (Morris et al. 1991). Herring gulls have been observed predating the eggs and chicks of all Great Lakes colonial piscivore bird species (Parsons 1971; Quinn 1981; H. Blokpoel, P.J. Ewins, R.D. Morris, J.S. Quinn, and D.V. Weseloh, personal observations). Two pairs of herring gulls nesting in the midst of the Hamilton Harbour ring-billed gull colony in 1992 inflicted heavy losses on adult ring-billed gulls (J.S. Quinn, personal observations). At one point 45 dead ring-billed gulls, some with their stomachs removed, were counted within a 3 m radius of one herring gull nest. Specialist bird predators have been described in a number of studies of herring gulls (Morris et al. 1992) and other species.

Ring-billed gulls

Nesting chronology and nest sites

Peck and James (1983) report the earliest egg-laying date in Ontario to be 14 April. In the areas surrounding the Caspian and common tern colonies in Hamilton Harbour, the first ring-billed gull eggs observed in 1994 were laid April 17 and April 19, respectively.

Most ring-billed gull colonies in Ontario occur on islands in the Great Lakes, the St. Lawrence and Ottawa rivers, and James Bay. Some colonies surround nesting herring gulls, common terns, or Caspian terns. Nests are typically raised mounds or platforms variously formed of grasses, plant stalks, aquatic plants, mosses, sticks, fish bones, or feathers (Peck and James 1983). Though sometimes using barren sites, nests are usually positioned in grasses, weeds, shrubs, and other vegetation. Although ring-billed gulls will nest almost anywhere, providing there are others nesting nearby, those initiating the earliest nests often choose piles of rubble and sites with much visual relief such as vegetation, driftwood, rocks, etc. (Ryder 1993). On South Limestone Island in Lake Huron's Georgian Bay, a limestone knoll that is vegetated mainly by a low profile species of cinquefoil (*Potentilla norvegica*) remains unused by nesting ring-billed gulls and is available for the later arriving Caspian terns (J.S. Quinn, personal observations). The gulls nest in a dense colony among the stands of stinging nettle (*Urtica dioica*) surrounding and on the edges of the knoll. Ring-billed gulls will sometimes nest in open areas with prostrate vegetation (P.J. Ewins, personal observations).

Ring-billed gulls nested in dense subcolonies on Pier 27 in areas unoccupied by herring gulls and over most of Pier 26 as well as at the Windermere Basin and Neare and Farr Islands (Fig. 1). Gull control was attempted at the southern end of Pier 26 and all of Pier 25 by the Hamilton Harbour Commissioners through extensive scaring operations utilizing crackers, propane cannons, ultrasonic – high pitch broadcasts, and all-terrain vehicles which appeared to reduce the density of nesting gulls drastically in the area of disturbance, although there were no control areas with which to compare.

Demography

The population of ring-billed gulls has exploded in the Great Lakes, increasing from about 56 000 pairs in 1976 to about four times that number in 1990 (Blokpoel and Tessier 1991). Ring-billed gulls first nested in Hamilton Harbour in 1978 when 78 nests were found. The most recent count, in 1990, put the Hamilton Harbour colony at 39 621 nests (Moore et al. 1995). This represents approximately 14% of the population of the lower Great Lakes (Blokpoel and Tessier 1991).

Interactions with other species

Ring-billed gulls nest earlier in the year than either of the tern species (see Morris et al. 1992), thus reducing tern nest-site availability. Ring-billed gulls are believed to have caused the abandonment of common tern colonies in Hamilton Harbour (Moore et al. 1995) and numerous sites on the lower Great Lakes (Courtney and Blokpoel 1983). Displacement of Caspian terns by ring-billed gulls has not yet been demonstrated clearly (Blokpoel and Tessier 1986).

Ring-billed gull predation of eggs and chicks of Caspian (Quinn 1981; Quinn and Morris 1986) and common terns (Morris et al. 1992) may be of concern in some cases. Close observation of Caspian and common tern colonies has revealed that predation by gulls may be due to one or a few individuals. Recently, in Hamilton Harbour, J. Sirdevan (personal observations) witnessed the complete loss of eggs from over 15 Caspian tern clutches to predation by the same individual ring-billed gull. The predatory gull followed a characteristic pattern for predation and consumption of the eggs. Following the shooting of that gull (under CWS permit), egg losses to that part of the colony stopped.

Common terns

Nesting chronology and nest site

Peck and James (1983) provide 8 May as an early egg-laying record for the lower Great Lakes. At Hamilton Harbour from 1991 through 1994, first eggs of the year were laid between 5 and 12 May (D. Moore, personal communication). Common terns normally initiate nesting approximately 3 weeks later than ring-billed gulls at this and other colonies (Morris et al. 1980, 1992).

Common terns breed on islands and shores and in marshes of lakes and rivers (Peck and James 1983). Nests are typically depressions, though some are flat or raised, consisting of simple to elaborate bowls of vegetation (Peck and James 1983). Nests are built on or in rocks, sand, and gravel, among various herbaceous plants, among driftwood, etc. Both descriptive (Blokpoel et al. 1978) and experimental (Richards and Morris 1984) studies of nest locations showed that colonizing birds preferred to nest near plants or other objects.

Demography

Common tern numbers in the Great Lakes have been in decline since the early 1970s with reductions in numbers of breeding birds at some sites, and entire colony desertions at others (Morris and Hunter 1976; Courtney and Blokpoel 1983; Blokpoel and Scharf 1991; Morris et al. 1992). Additionally, the Great Lakes population appears to be demographically separate from the thriving East Coast population. During the period from the early 1920s until 1976, only four movements of

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banded birds into the Great Lakes from the East Coast of North America were recorded (Haymes and Blokpoel 1978), suggesting that the Great Lakes population represents a distinct genetic stock. The Hamilton Harbour population, numbering 954 nests in 1993 (Moore et al. 1995) represents over 40% of the lower Great Lakes population, which totalled 2348 nests in 1990 (Blokpoel and Tessier 1991).

Interactions with other species

Common terns are most often the victims in their interactions with other species dwelling near common tern colonies. They are subject to loss of eggs, chicks, and nesting habitat by ring-billed gulls (Morris et al. 1992); predation of chicks and adults by herring gulls (Morris et al. 1991); and loss of young by black-crowned night-herons (Hunter and Morris 1976) or the nocturnal desertion of adult terns due to night-heron disturbance (Shealer and Kress 1991). In addition, available nesting substrate can be lost to earlier nesting ring-billed gulls (Morris et al. 1992).

Caspian terns

Nesting chronology and nest site

Clutch initiation began in Hamilton Harbour 6 May 1994 (J. Sirdevan and J.S. Quinn, unpublished data) concurring with the early egg date listed in Peck and James (1994). Ring-billed gull egg laying began 14 April in the vicinity of the Hamilton Harbour Caspian tern colony and ring-billed gull breeding was advanced well into incubation at the time the first Caspian tern eggs were laid (J. Sirdevan and J.S. Quinn, unpublished data).

Caspian terns nest in dense colonies in the Great Lakes, often in association with ring-billed or herring gulls. Their nests consist of a depression in the substrate scraped out with their feet and occasionally lined with plant material, pebbles, and fish bones. J.S. Quinn and J. Sirdevan (unpublished data) found a clear preference for sand when terns were given a choice of three substrates: 1 cm crushed stone, pea gravel, and construction grade sand. Caspian tern colonies typically are in very open and largely unvegetated areas (Peck and James 1983). When vegetated, the vegetation is typically sparse and prostrate. H. Blokpoel (personal observations) observed that Caspian terns on Pigeon, Little Galloo, and Gull islands nested on the muddy margins of interior ponds after they had dried out during the spring. These areas were too wet to be used earlier in the season when ring-billed gulls initiated their nests. Caspian terns have nested in Hamilton Harbour since 1986, forming one to three subcolonies each year in the Pier 26–27 areas. In 1993 and 1994, one to six late-nesting pairs nested on a sand-covered raft designed for Caspian terns and anchored in the southern confined disposal facility (Fig. 1) near one subcolony location (Lampman et al. 1996).

Demography

Following the establishment of a colony of 48 nests in 1986, numbers have generally increased and appear to have stabilized at about 300 pairs in one to three subcolonies. The establishment of additional subcolonies and an apparent increase in nesting density at the main subcolony may have been necessitated by the encroachment of ring-billed gulls and vegetation in the vicinity of the main colony site located about 100 m north of the Pier 25 docking facilities (J.S. Quinn, personal observations). The Hamilton Harbour subcolonies collectively represent the fourth largest of five Caspian Colonies in Lake Ontario in 1994 (Moore et al. 1995). In the Great Lakes, Caspian tern nesting numbers have increased steadily from 1995 pairs in 1963 (Ludwig 1979), to about 5700 pairs in 1987 (Blokpoel and Scharf 1991). Mean annual increases between the late 1970s and early 1990s have been highest on Lake Ontario (23% per annum; Ewins et al. 1994). These increases have been attributed to a combination of declining contaminant burdens and to increased availability of forage fish (Ewins et al. 1994). Caspian terns are a species of concern in the Great Lakes according to Canadian and U.S. agencies (Blokpoel and Scharf 1991).

Interactions with other species

Caspian terns begin nesting about 2 weeks after ring-billed gull colonies have become well established (J.S. Quinn, personal observations). Nesting is excluded from areas occupied by high densities of gulls. Their colonies are typically located in areas devoid of vegetation that would provide vertical structure or reduced visibility and with few gulls on the immediate site. While this may reflect some preference on the part of Caspian terns, recent indirect evidence that ring-billed gulls may prefer nesting near vertical structure (described below) suggests the possibility that Caspian terns avoiding tall vegetation may be due to the avoidance of such areas by ring-billed gulls.

Predation of Caspian tern eggs and chicks by both ring-billed gulls (Quinn and Morris 1986; P.J. Ewins, personal observations) and herring gulls (Quinn 1981; P.J. Ewins, personal observations) has been observed. Presumably because of gape limitations, ring-billed gulls were implicated in taking only young Caspian tern chicks (Quinn and Morris 1986), while herring gulls were observed to take chicks of at least 21 days of age (J.S. Quinn, personal observations; Quinn 1981). Egg predation by ring-billed and herring gulls can be exacerbated by humans disturbing Caspian tern colonies (Quinn 1984; P.J. Ewins, personal observations).

Discussion

Conservation issues

We have identified five key factors that require short- and long-term management attention. These include (*i*) vegetational succession, (*ii*) habitat modification by birds, (*iii*) interspecific competition for nesting space, (*iv*) predation by birds, and (*v*) human disturbance. First, successional changes in vegetation may alter the suitability of nesting habitat for both ground-nesting and tree-nesting species. Vegetational succession is known to cause changes in occupancy by island-dwelling colonially nesting waterbirds (Parnell et al. 1988). Successional encroachment of herbaceous plants appears to inhibit nesting by common terns (Morris et al. 1992). Such changes in habitat may have a similar effect on Caspian terns, although it is difficult to discount the confounding influence of nest-site competition with ring-billed gulls (see below). The two gull species are better able to cope with advancing successional stages (Blokpoel and Tessier 1986).

Second, activities of the birds themselves can significantly modify the structure of the habitat. Of the species noted here,

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Table 1. Summary of substrate and vegetation plans and short-term management plans for the artificial islands.

Island	Habitat features	Short-term management plans
North	Overall barren, without topsoil; 200-m^2 knoll on northern end for Caspian terns; 250-m^2 area topped with mixed sand and gravel with scattered driftwood and larger stones on southern end for common terns	Tern nesting habitat to be covered or patrolled (ring-billed gull nests destroyed) until terns begin nesting; vegetation on Caspian tern site to be controlled, if necessary
Centre	Southern third surfaced with topsoil, planted with native trees and shrubs; northern two-thirds barren; 250-m^2 area on northern end for common terns (see above); 250-m^2 area along northern edge of planted area with "decoy nests" for ground-nesting cormorants; black-crowned night-herons may be attracted to shrubs and trees	Common tern area covered or patrolled (to restrict or remove ring-billed gull nests); cormorant nests removed from trees
South	Surfaced with topsoil and planted with trees and shrubs; shrubs planted along shore to attract black-crowned night-herons	Double-crested cormorants will be discouraged from nesting

cormorants provide the best example as their acidic guano can kill vegetation. Such death and resultant toppling of nesting trees at some breeding sites, including Hamilton Harbour, has reduced tree-nesting sites (Weseloh and Ewins 1994; Weseloh et al. 1995). The result of this loss of habitat has been a shift at some cormorant colonies in the lower Great Lakes to nesting on the ground, sometimes displacing herring gulls, or in low bushes, where they may displace black-crowned night-herons.

Third, nest-site competition among ground-nesting species favours earlier nesters such as ring-billed gulls over later nesting species such as terns. Habitat that is acceptable to earlier nesting species will be unavailable for later nesters unless they are sufficiently large and aggressive to take over occupied nesting sites. Of the species in question, we know of only one, double-crested cormorants, for which we have data showing that takeovers of occupied territories occurs, specifically cormorants taking over occupied herring gull nests (P.J. Ewins, personal observations). Suitable nesting habitat can be preserved for late nesters by blocking access by early nesters (e.g., covering with materials to prevent access) or removal or deterrence of the earlier nesting species (see examples for preservation of common tern habitat in Morris et al. 1992).

Fourth, predation by one colonially nesting species on another may reduce the nesting success of the prey species. Egg-eating ring-billed gulls have been observed and removed (under Canadian Wildlife Service permit) after extensive predation of common tern (Morris et al. 1992) or Caspian tern eggs (J.S. Quinn, personal observations). In both instances, egg predation stopped after the removal of one to three egg-specialists. Losses of eggs to gulls may be exacerbated by human disturbance, although such losses during research can be reduced by the use of "nest domes" to cover vulnerable eggs (Quinn 1984).

Finally, human disturbance of colonial nesting birds can reduce breeding success (see Parnell et al. 1988). Such disruptions may result in the temporary abandonment of tern, cormorant, or night-heron colonies leaving the nest contents exposed to gull predators or inclement ambient conditions. Disturbances during the nestling period may induce the scattering of mobile offspring and subsequent attacks by conspecific adults as displaced young attempt to find their way back (Fetterolf 1983). Disturbances on small islands with insufficient cover during periods of chick mobility may lead to the offspring of ground-nesting species swimming off and getting lost, drowning, or dying of exposure.

Each of these five factors is taken into consideration in our discussion of habitat design and management procedures that follows.

Habitat design

The design and management of the islands will require the cooperation of avian biologists and parties associated directly with the Fish and Wildlife Habitat Restoration Project team of the Hamilton Harbour RAP. The following discussion represents our proposal for management and fine-scale island design given the rudimentary plan determined previously by the Fish and Wildlife Habitat Restoration Project team, following recommendations pertinent to waterbirds from three of us (R.D.M., J.S.Q., and D.V.W.). The three artificial islands will be suitable to differing extents for the six colonial species because of substrate and vegetation differences (Table 1). The location and structural design of the islands has been finalized (Mar-land Engineering Ltd. 1994[4]). Each of the islands has been designed so that they will not be washed over during storm events. The basic landscaping of the islands is in the advanced planning stages and we assume will not change substantially (Fig. 2). The southern island will be surfaced with topsoil and planted with native trees and shrubs. The centre island will remain devoid of topsoil on its northern end while the southern portion will be covered with topsoil and planted with native shrubs. The northern island will remain devoid of topsoil and will not be planted.

The challenge and intent of the design plan is to encourage the terns and night-herons while restricting the dominating impacts of ring-billed gulls and double-crested cormorants. All authors are fully aware of the risks posed by investigators to eggs and chicks of breeding waterbirds (see for example Parnell et al. 1988; Brown and Morris 1995), and will conduct management procedures appropriately. For readability, we present our proposed management plan as if already approved and as if we will be responsible for implementation.

We will accommodate double-crested cormorants on the centre island using a strategy intended to reduce cormorant impact on night-herons and cormorant damage to trees. This island will provide 250 m^2 of ground-nesting habitat, sufficient for about 250–500 pairs of cormorants, assuming an area of 0.5–1.0 m^2 per pair. Ground-nesting will be encouraged in the middle region, north of the vegetated part of the island

[4] Mar-land Engineering Ltd. 1994. Project No. 410-201. c/o Mr. J. Hall or Hamilton Harbour Commissioners, 605 James Street North, Hamilton, ON L8L 1K1, Canada.

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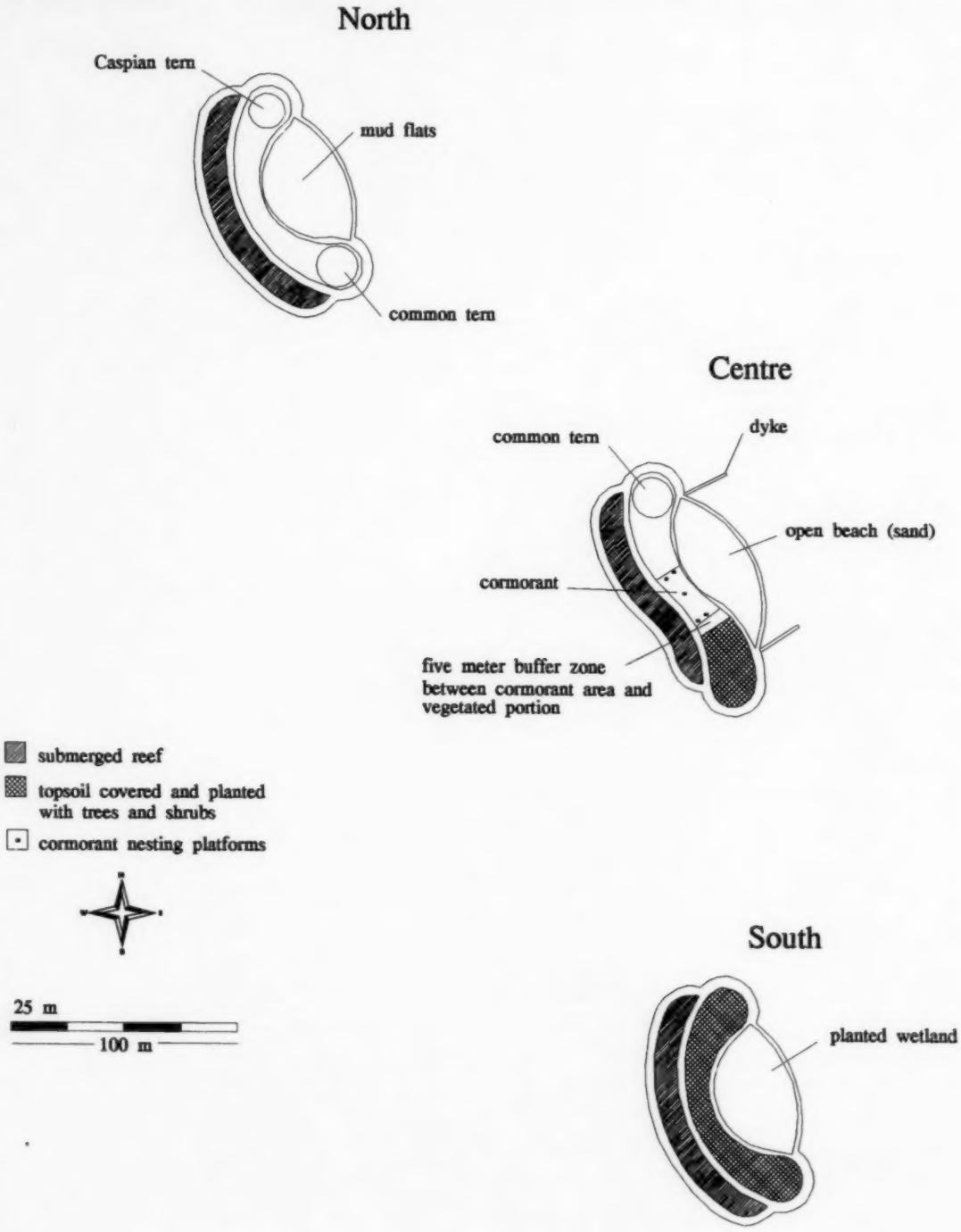
Fig. 2. Site plan for three wildlife islands near the northeastern shoreline of Hamilton Harbour, with proposed nesting sites for colonially nesting waterbirds.



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(Fig. 2). To allow easy access to the colony site by cormorants we recommend that short ridges be constructed along the east and west shore adjacent to the colony site. The provision of these ridges, providing a 60° slope down to the water will facilitate cormorant take-offs and will increase the suitability of the site. In addition, the plan calls for the erection of five artificial nesting structures that will be placed temporarily in the area designated for cormorant ground nesting. These accessories are intended to attract cormorants to nest in the designated area before trees on the islands are large enough for cormorant nesting. Nesting structures described by Meier (1981) consist of platforms supported by a wooden pole. In our plan, each pole would extend 6 m above the island's surface (Meier (1981) describes 9 m poles) and would provide eight platforms. To encourage ground-nesting by cormorants at the new location, we intend to move existing and previously used cormorant ground nests from the current site in Hamilton Harbour to the area under the poles. As the platforms are occupied by nesting cormorants, we expect pairs to begin nesting on the ground near the nesting structures. Once a group of ground-nesting pairs has been well established, we will remove one or two of the poles from the island each autumn until none remain. The removal of poles will improve the aesthetic appearance of the islands and should facilitate our attempts to discourage tree nesting by cormorants on the wildlife islands. To reduce damage from cormorants breaking branches for nest building, and to reduce the likelihood of tree-nesting in later years, we propose that a 5-m buffer zone between the cormorant colony and the vegetated part of the island be maintained by removal of nests prior to egg laying. If cormorants begin damaging the young trees, we will provision them with sticks for nesting. If necessary, young trees will be covered with netting to prevent damage by cormorants. Once trees have matured it may become necessary to discourage tree nesting by removing cormorant nests from trees as early as possible. For aesthetic reasons and to encourage other tree nesters including black-crowned night-herons, we hope to encourage tree growth. However, it is possible that cormorants will prove too destructive. Aside from Meier's (1981) report describing just the artificial nesting structures, there is no known precedent for our approach.

Predation of cormorant eggs by ring-billed and herring gulls can be a serious problem during human disturbance; cormorants flush from their nests and gulls fly in and eat the unprotected eggs. Predation by gulls can be reduced dramatically by restricting researchers' colony visits to periods of darkness (K. Stromberg, U.S. Fish and Wildlife Service, personal communication).

Habitat suitable for black-crowned night-herons will be created on the southern and centre islands. Plantings of red-osier dogwood (*Cornus sericea*); peach leaf willow (*Salix amygdaloides*), previously used as nesting habitat by black-crowned night-herons; and other low shrubs will provide sufficient cover and structure for nesting black-crowned night-herons. The creation of stands of these shrubs may encourage night-heron nesting and is likely to discourage predation of night-heron eggs and chicks by gulls. Cormorants are less likely to nest in these small shrubs, specifically chosen for planting on the islands because of their small growth form when mature.

Ground-nesting species with particular habitat requirements are the focus of our habitat design considerations for the surfacing of the artificial islands. Since both gull species are effective at establishment and maintenance of colonies, we assume that they will nest without the need for any special habitat modification.

The design and management challenge posed by ground-nesting gulls and terns is to restrict gull nesting from areas targeted for terns. The habitat designed for use by common terns will need to be protected from occupancy by nesting gulls. Experimental studies by Richards and Morris (1984) and observational studies by Blokpoel et al. (1978) both demonstrate that common terns prefer to nest on small-sized gravel or chip substrate, often near plants, rocks, and logs. Furthermore, terns nesting on such enhanced substrates had larger clutches and higher hatching and fledging success than those nesting on adjacent substrates without these (Richards and Morris 1984). This difference was attributed to the greater visibility of eggs and chicks to predators on the sites lacking structure provided by logs and plants. We propose to create approximately 250 m^2 of common tern habitat at the northern tip of the unplanted portion of the centre island as well as at the southern tip of the north island. Assuming 0.25 m^2 per pair (R.D. Morris, personal observations), this is sufficient space for 1000 pairs of common terns at each colony site. The area will be surfaced with a mixture of sand and gravel, with driftwood and larger stones scattered over the area and low herbs such as *Potentilla simplex* or *P. canadensis* planted over the area. The habitat will be kept free of nesting gulls by regular daily or twice daily human patrols from early April (when gulls start building nests) until mid-May (when common terns begin nesting). During these patrols, all gull nests on the tern-designated area will be destroyed.

In concert with new common tern habitat created on the islands, we strongly recommend the protection and encouragement of the common terns already nesting on the "spur dyke island" in the Windermere Basin. Management procedures include covering of the entire dyke substrate with plastic sheeting early each season and destruction of any gull nests started on the dyke. In 1993 and 1994, common terns nesting on the spur dyke island in Windermere Basin were more successful than those nesting on the mainland surrounding the Windermere Basin (H. Blokpoel, K. Lampman, and D. Moore, personal observations). If possible, the construction of new spur dyke islands in Windermere Basin would provide important additional habitat for common terns. In addition to maintaining the spur dyke for occupancy by common terns, we plan to anchor tern rafts in the Windermere Basin to increase insular nesting space for common terns as a short-term measure. These small rafts have been used successfully by small numbers of nesting common terns elsewhere in the Great Lakes (Dunlop et al. 1991; Morris et al. 1992; H. Blokpoel, personal observations).

Previous studies of Caspian terns suggest specific habitat design components. During experiments for substrate preference with Caspian terns at Hamilton Harbour in 1994 (J.S. Quinn and J. Sirdevan, unpublished data), ring-billed gull nest construction was interrupted immediately upon discovery. The nesting material was disturbed and scattered away from the immediate vicinity of the nest site by a field assistant who patrolled the site of the 1993 main Caspian tern colony several times a day (under Canadian Wildlife Service permit) starting

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Table 2. Proposed methods to manage the six main species of colonial waterbirds on artificial islands in Hamilton Harbour.

Species	Encouragements to nesting	Discouragements to nesting
Double-crested cormorant	Install nesting platforms; move ground nests from mainland site to island site	Remove nests from trees and shrubs
Black-crowned night-heron	Plant shrubs; install decoys; remove cormorant nests from trees and shrubs	None
Herring gull	None	Removal of nests in tern-nesting areas
Ring-billed gull	None	Removal of nests in tern-nesting areas
Common tern	Provide gull-free substrate; install visual relief objects; install decoys; broadcast sounds; install chick shelters	None
Caspian tern	Provide gull-free substrate; create dry sandy knoll with low-profile vegetation; install decoys; broadcast sounds	None

from 5 April until 11 May. Nest initiations were common and persistent throughout the area, which had begun to be invaded by a number of plant species. However, the site of the substrate preference experiment, which was devoid of vegetation, was virtually ignored by the gulls as a nesting area. Over the entire period of nest removal, only two gull nests were initiated on the 9×9 m plot despite the frequent initiation of numerous gull nests in the vegetated area within 2 m of the experimental plot (J.S. Quinn and C. Pekaric, personal observations). In sharp contrast, 19 of the first 20 Caspian tern nests were initiated on the experimental plot, and only one on the existing partly vegetated substrate (J. Sirdevan and J.S. Quinn, unpublished data). These data suggest that substrate devoid of tall vegetation may serve to attract Caspian terns and repel ring-billed gulls.

Caspian terns will be encouraged to nest on a 200-m^2 knoll raised about 1 m above the highest part of the north island. The knoll will be surfaced with a mixture of mainly sand and some pea gravel, planted with a low-lying xerophytic plant such as *P. simplex*. The knoll should be well drained and unsuitable for herbaceous plants with significant moisture requirements. Under these conditions we expect the knoll to be the least vegetated part of the island and so reduce the tendency for ring-billed gulls to nest on the knoll. Controlled experiments planned to be undertaken in 1995 by J.S. Quinn and J. Sirdevan will evaluate the effect of a lack of vegetation on ring-billed gull and Caspian tern nesting. If necessary, gulls will be prevented from nesting on the knoll by patrolling and removing gull nests or by placement of plastic sheeting over the area until early May when Caspian terns are about to nest. We expect that the knoll will be eventually surrounded by nesting gulls.

Attraction to sites

With the provision of suitable habitat, we assume that pairs of the six species of breeding waterbirds will colonize the islands naturally; there will be no effort to restrict their access to mainland nesting sites unless the Hamilton Harbour Commissioners forecast construction on existing mainland colony sites. Tern habitats on the islands will be groomed and prepared and decoys placed along with speakers and tape recordings of tern calls. Decoys have been used successfully to attract least terns (*S. antillarum*; Kotliar and Burger 1984), and decoys and tape recordings have been used to attract nesting common terns, arctic terns (*S. paradisaea*; Kress 1983), little blue herons (*Egretta caerulea*), and cattle egrets (*Bubulcus ibis*; Dusi 1985). Prior attempts to attract Caspian terns with decoys and playback were met with equivocal results (D.V. Weseloh, P.J. Ewins, and H. Blokpoel, personal observations). There will be no further effort to dissuade birds from nesting at mainland sites for 4–6 yr unless plans to develop the nesting sites are forecast within this time frame.

In the event that colonization does not occur over a period of 4–6 yr, or if imminent development dictates, we will dissuade birds from nesting on the mainland while attracting them to their respective prepared sites. Assuming advance notice of development plans, we will attempt to move at least Caspian and common tern pairs in the year preceding development.

Common terns attempting to nest on all mainland areas surrounding Windermere Basin will be disturbed on a regular basis from their first arrival in mid-April. With the cooperation of the Hamilton Harbour Commission and required Canadian Wildlife Service permits, regular truck traffic will be rerouted to run along the dykes separating settling ponds, and human patrols will supplement disturbance caused by trucks. As the spur dyke island fills with nesting pairs, we anticipate displacement of remaining pairs to the new island sites.

Within 5 days of the first Caspian tern clutch initiations researchers will cover the largest of the mainland Caspian tern subcolony sites with polyethylene and continue broadcasting the playback at the proposed new colony site. We anticipate that Caspian terns, ready to oviposit, will be attracted to the proposed Caspian tern site.

Short-term island management

Short-term management goals will be to maintain gull- and cormorant-free nesting habitat for terns and night-herons (Table 2). Caspian and common tern breeding areas will be covered with plastic sheeting and be regularly patrolled to prevent ring-billed gull nest establishment. We will minimize our control procedures on gulls at other locations unless other species are being compromised by nest-site competition or extensive predation. As they have been shown to reduce gull predation on common tern chicks, shelters (Burness and Morris 1992) will be placed adjacent to all nests at the tern colonies prior to egg hatching. During researcher visits to the colonies, nest domes will be placed over tern nests for the protection of eggs and young chicks (Quinn 1984). Excessive levels of gull predation on the eggs or chicks of terns will be considered on a case by case basis. When successful nesting of significant numbers of pairs is known to be compromised, predatory individual(s) will be eliminated under permit. Finally, the control of noninvestigator human disturbance will require the

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posting of signs on the islands, at local marinas, and at public boat ramps during the breeding season. Patrolling of the islands may be necessary to enforce signing.

Long-term management and philosophical considerations

The establishment of breeding colonies on artificial islands in Hamilton Harbour will not automatically maintain waterbird biodiversity in the region; continuing efforts to monitor and manage the islands are essential. Routine censusing of all colonially nesting species on the islands, in concert with detailed studies of the breeding success of less abundant species (especially the terns and night-herons), will provide an early warning of developing problems. If problems are detected, careful studies would be implemented to determine the primary factors and possible solutions. We recommend that research-related disturbance be minimized on the islands during the first few years of colony establishment.

In the event that the ring-billed gull or double-crested cormorant populations become sufficiently large to threaten the continued existence of other colonial species, long-term population control is recommended. Although labour intensive, the annual application of mineral oil to the eggs of all clutches in the control area is a measure intended to reduce recruitment into the population and would be expected to cause the numbers to decline over the period of several years (Morris and Siderius 1990; Christens and Blokpoel 1991). Previous work with the technique showed that ring-billed gull pairs continued incubating their oiled clutch, containing eggs with dead embryos, for up to 6 weeks beyond the usual incubation period (Morris and Siderius 1990). These pairs did not renest during that breeding season and so recruited no young into the population. Such drastic action would require careful consideration but would need to be set into action early to avoid the loss of species at risk. This need for early action underscores the necessity of monitoring the success of some species.

One important, yet often neglected, component of conservation addresses the issue of overabundance (Garrott et al. 1993). Species that can adapt and thrive in human-altered environments can be devastating to less adaptive and sensitive species. Accordingly, conservation biologists must be prepared to confront the problem of overabundance of some species to avert numerical losses in others. Extreme views on the ethical justifiability of management contrast the passive with the proactive approach to human interaction with nature. Anthropomorphists such as Norton (1986) hold that humans are the source of all value and that the value of non-human lifeforms ought to be determined as favourable or nonfavourable to objectives established by the human manager. Conversely, non-anthropocentrists such as Katz (1985) state that species reductions or replacements that occur by natural processes are acceptable; artificial reductions or replacements (i.e., management of resources) are not acceptable as they cannot be justified on philosophical grounds. The recent dramatic population number increases of ring-billed gulls and double-crested cormorants are attributable largely to human activities (Blokpoel and Tessier 1986, 1988; but see Southern 1987, 1988; Ewins 1994; Weseloh et al. 1995). This being the case, management that reduces the impact of inflated numbers of ring-billed gulls and double-crested cormorants may be viewed as partially correcting a human-caused problem. Here we adopt a philosophy of management for the expressed purpose of maintaining colonial nesting species diversity both locally and in the Great Lakes. We accept the responsibility of actions that may be detrimental to ring-billed gulls or double-crested cormorants to the benefit of other species.

[5] International Joint Commission. 1991. Review and evaluation of the Great Lakes RAP: remedial action plan program 1991. International Joint Commission, Windsor. Available from Library, Canadian Centre for Inland Waters, Box 5050, 867 Lakeshore Drive, Burlington, ON L7R 4A6, Canada.

Concluding remarks

Efforts directed towards habitat creation on artificial islands, establishment of bird colonies on those islands and their maintenance on currently used sites, and appropriate long- and short-term management of Hamilton Harbour's colonial nesting birds will help to maintain colonial waterbird species diversity. Continuing studies are expected to provide data for refining the approaches suggested here. Hamilton Harbour's RAP appears to be ahead of most of the other 18 RAPs in the 43 Areas of Concern designated by the International Joint Commission (1991[5]). The techniques and strategies tested here will provide information that should be applicable to other areas with colonial waterbird populations undergoing remediation in human-altered aquatic ecosystems.

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Historic and comparative perspectives on rehabilitation of marshes as habitat for fish in the lower Great Lakes basin

Thomas H. Whillans

Abstract: Retrospective and comparative assessments of fish habitat have been used to guide rehabilitation in Cootes Paradise, a marsh at Hamilton, Ont., on Lake Ontario. The marsh was severely altered by human and natural stresses, including high water levels, influx of fine eroded sediments, and channelization. Recovery has been limited by a different but overlapping set of stresses, including the continued influx of fine eroded sediments, resuspension of sediments, exotic fish, and increased fetch. Assessment has involved the use of "accumulator-," "residue-," and "replica"-type retrospective evidence and the comparison of Cootes Paradise with other reference marshes. The emergent narrative science (a synthesis of science in historical and environmental context that serves as a partially testable hypothesis), verified and adjusted by small scale experiments, has identified the need to re-introduce vegetation, reduce fetch, exclude common carp (*Cyprinus carpio*), anchor the marsh sediments, and reduce the influx of land use derived fine sediments. Narrative science uses the "ecological memory" of the marsh for historical information on ecological degradation and in the form of the remnant natural resilience upon which ecological rehabilitation could build. The narrative science provides the basis for adaptive management and the monitoring that it requires.

Résumé : Des évaluations rétrospectives et comparatives de l'habitat du poisson ont servi à guider les travaux de restauration du marais Cootes Paradise à Hamilton, sur le lac Ontario. Le marais avait été gravement perturbé par des agressions humaines et naturelles, notamment le haut niveau de l'eau, l'apport de sédiments d'érosion fins et le creusement de chenaux. Le rétablissement a été limité par une série différente mais simultanée d'agressions, notamment la poursuite de l'apport de sédiments d'érosion fins, la remise en suspension des sédiments, la présence d'espèces exotiques et l'augmentation du fetch. Nous avons eu recours pour l'évaluation à des justifications rétrospectives de type "accumulateur", "résidu" et "réplique", et à la comparaison de Cootes Paradise à d'autres marais de référence. Grâce à la nouvelle approche narrative (synthèse de la recherche, inscrite dans son contexte historique et écologique, qui sert d'hypothèse partiellement vérifiable), après vérification et ajustement par des expériences à petite échelle, nous avons relevé la nécessité de réintroduire de la végétation, de réduire le fetch, d'éliminer la carpe (*Cyprinus carpio*), d'ancrer les sédiments du marais et de réduire l'apport de sédiments terrigènes fins. L'approche narrative utilise la "mémoire écologique" du marais pour obtenir des données historiques sur la dégradation écologique et pour mesurer la résilience naturelle résiduelle sur laquelle pourra s'appuyer le rétablissement écologique. Cette approche scientifique donne une base pour une gestion adaptative et pour la surveillance que cette gestion nécessite.
[Traduit par la Rédaction]

Introduction

Ecological conditions are expected to change through time and across space. Often, both types of change can be explained in the same way. Succession in a vegetational community could, for example, be characterized as a change through time at a particular location or as a change across space, each related to soil organic content. This paper shows how, with respect to Cootes Paradise at Hamilton on Lake Ontario, retrospective and comparative science have been combined to understand change in marsh habitat of fish and to prioritize steps in rehabilitation of that habitat.

Ecologists must understand the conditions or functions that they are attempting to rehabilitate. Retrospection is more defensible than spatial comparison for this purpose because of its immediate geographic relevance. However, space can be substituted for time to investigate ecological processes. Ecological rehabilitation is often a response to cumulative effects of human activity. Cumulative effects have been defined as many small impacts combined additively or synergistically over time or across space (Canadian Environmental Assessment Research Council 1988). This paper is, thus, directly applicable to the assessment of cumulative effects. However, as will be illustrated, the process of habitat restoration is often not simply a matter of eliminating degrading influences. Factors limiting the recovery of habitat can differ from those that degraded it. Both types of factor must be addressed unless the latter have decreased sufficiently.

The challenge is to characterize ecological conditions and functions that existed prior to degradation. Interpretation can be based on the "ecological memory" of a site, i.e., the patterns and features that are evidence of processes and actions that prevailed in the past and that are often fundamental determinants of the future. The "narrative reconstruction" of past bio-

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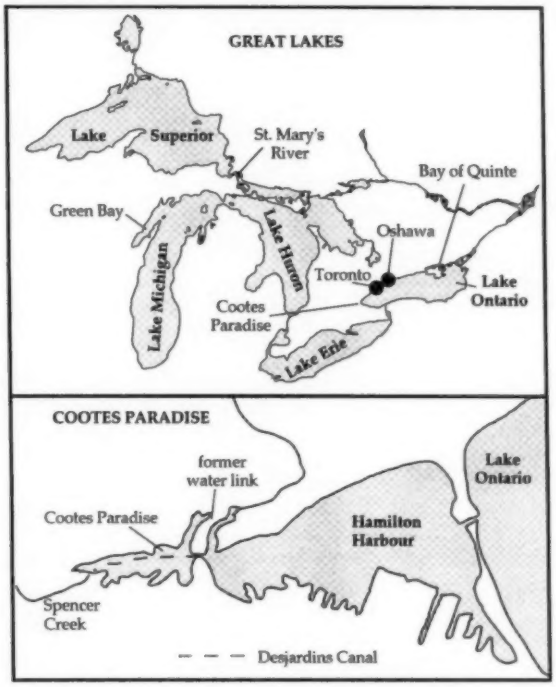
Fig. 1. The Cootes Paradise retrospective case study situation and comparative sites.



physical conditions becomes the ecological benchmark against which evidence of later change could be registered. Also, the understanding of past ecological functions that is expressed in the narrative is useful for developing models for rehabilitated ecosystems.

Approaches to retrospective assessment

Three types of "retrospective assessment" have been used: monitoring, modelling, and hindsight analysis. Retrospective monitoring, the focus of this paper, is the use of proxy, remnant, or residual data to document circumstances after they occurred. Modelling is extrapolation backwards from an information series, or analysis of a data series, to reveal a hypothetical relationship. Hindsight analysis typically evaluates programs or projects in terms of their stated intentions. Each type of retrospection is served by a set of tools that is shared partially with the others. Retrospective tools have been summarized by Whillans (1985), Smol and Glew (1992), Smol (1995), and for monitoring by the Monitoring and Assessment Research Centre (1985).

Accumulators, residues, and replicas are direct evidence of past environments. Accumulators record environmental change by storing a by-product of the change at a regular rate, most usefully when proportional to its intensity. Examples would include contaminants in biological growth tissues and atypical year-class sizes in the population structure of long-lived animals (Beamish and Harvey 1972; Wong and Whillans 1973; Sheppard and Funk 1975). Residues are those remnants of previous environments that have survived relatively intact by design or accidentally. Examples include archaeological remains or cores of undisturbed sediment laden with diatoms or pollen (Watts and Winter 1966; Smol and Glew 1992; Hoffmann 1994). Replicas are images, data, or descriptions of the past deliberately created by researchers for specific purposes but that might also be used in other ways. Examples include creel census data and historical aerial photographs (Whillans et al. 1990; Haras et al. 1976).

Interpretation of evidence can be aided by dating techniques, ecological indicators, observations across spatial gradients, and numerical and biophysical simulation models (Smol 1992). Ideally, retrospective assessment involves work with two or more types of retrospective tool: first, screening broad rehabilitation issues and, then, iterating between the retrospective broad screen and hypothesis testing.

When a marsh is suspected to be experiencing human-generated ecological change, the broad questions relating to fish habitat rehabilitation that might be addressed retrospectively include the following: (*i*) Has the marsh habitat indeed changed over time? (*ii*) Has the fish community changed over the same period? (*iii*) Have fish community or habitat changes occurred concurrently with intensification of natural or cultural stress? (*iv*) If the marsh conditions changed over time, was this related more to the intensification of stress or the failure to recover after the amelioration of stress? (*v*) What processes seem to be limiting ecological recovery? (*vi*) What would constitute full rehabilitation? (*vii*) What ecological components should be monitored to facilitate future retrospection?

The case of Cootes Paradise marsh

Fish habitat, particularly in marshes along the shorelines of water bodies, tends to experience natural variation in ecological conditions because of hydrological and other forces. For example, over a 10–15 yr period, water level fluctuation in the Great Lakes has historically had an amplitude in the order of 3 m. Marshes in water bodies with such marked hydrological fluctuations have been labelled as "pulse stable" or successional features (Odum 1969), features that information from one point in time could not explain adequately. Thus, natural ecologic cause–effect relationships can often be detected more easily over the long term than the short term, perhaps 50 yr for water level relationships in the Great Lakes.

Marshes along the shores of the lower Great Lakes have undergone substantial human-generated change, superimposed on natural variation. One such marsh is Cootes Paradise, immediately west of Hamilton Harbour at the west end of Lake Ontario (Fig. 1).

Cootes Paradise is a 250-ha marsh located between the mouth of Spencer Creek and a high sand and gravel bar that remains from postglacial Lake Iroquois. The marsh connects with Hamilton Harbour through a cut that was excavated between 1851 and 1854 (Kerr 1885). The natural connection with the harbour around the north end of the bar was filled in. The Desjardins Canal was dredged into Spencer Creek through the marsh between 1826 and 1833 (Ozanian 1957). The marsh is now mostly open water and unvegetated. Stands of emergent plants and floating-leaved plants exist in a few embayments. Water clarity is extremely low, generally much less than

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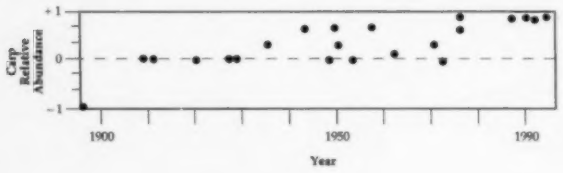
Fig. 2. Historic abundance of common carp in Hamilton Harbour and Cootes Paradise. On the scale of relative abundance 1 represents high abundance; –1, low abundance; and 0, that the species was reported as being common. The whole figure is standardized according to base-line points of low or high abundance that are authenticated by multiple sources. Data sources listed chronologically by time of observation: McCrimmon (1968), Sealey (1909), Hamilton Evening Times (1911), Hamilton Spectator (1953), Harkness (1927), Dymond et al. (1929), Dymond (1931), Lamoureux (1958), Students Burlington Beach Bungalow School (1943), Turner (1948), Kay (1949), Warren (1950), Lautens (1957), Lamoureux (1962, 1970), Veal (1972), R.A. Sonstegard (Department of Zoology, University of Guelph, Guelph, Ont., personal communication, 1977), G. Smith (Dundas, Ont., personal communication), and Randall et al. (1993).



40 cm Secchi depth (Painter et al. 1989), relating mostly to inorganic turbidity (Sager 1995).

The problem in Cootes Paradise is that the fish community is dominated by a few relatively undesirable species that can tolerate the current conditions of the marsh: high turbidity, open shallow water, predominantly silty substrate, widespread absence of aquatic vegetation, and exposure.

Has the marsh habitat indeed changed over time?

Change would be revealed as an unprecedented rate or scale of loss or gain of marsh habitat. Long-term variation in wetland area has been monitored effectively inland through the use of past surveys of organic soils (Snell 1987). The technique is not effective for shoreline marshes, because they were not generally included in soil surveys. Aerial photographs, historic maps, and sediment cores have proven more useful for detecting change in those marshes. In the lower Great Lakes basin, land-use changes spanning more than 2000 yr have been ascertained with deep water sediment cores (Warwick 1980), but the potential to detect change in marshes is limited by the availability of undisturbed nearshore sediments. Palaeolimnologic evidence from some fortuitously stable-bottomed marshes in the Lake Ontario watershed indicates that variation in vegetational conditions has been substantial over thousands of years in response to factors such as water levels (e.g., Yu and McAndrews 1994). Cores from Lake Erie marshes also reveal a dynamic vegetational composition (Terasmae 1970; Sherlock 1977; Whillans 1985). Cootes Paradise sediments have not been stable enough for reliable cores.

Approximation of the areal change over the past 200 yr is possible using historic maps. The area of emergent vegetation that is estimated from historic maps to have disappeared since the early 1800s in Cootes Paradise and Hamilton Harbour is 76% (Whillans 1982). The magnitude of loss is comparable with other urban areas along Lake Ontario. Comparatively minor change has been recorded along rural shorelines.

The major losses of marsh area in Cootes Paradise occurred in the 1900s, coincident with the period of coverage by aerial photographs. Emergent marsh area on 12 sets of aerial photographs dating from 1934 to 1985 revealed a sequential pattern of major losses followed by incomplete recoveries (Portt et al. 1991).

The Cootes Paradise findings were generated using a method of aerial photograph interpretation based on Whillans (1985) and comparable in approach to Lyon and Drobney (1984) and Bray (1993). These three studies along rural Lake Erie, rural Lake Michigan, and the more developed St. Marys River showed that sizeable fluctuations in vegetated wetland area correlated inversely with magnitude of water level. In contrast, Cootes Paradise experienced a progressive decline in vegetated wetland area after the mid-1900s, even though water levels oscillated. Thus, both the scale and rate of reduction of vegetated wetland area in Cootes Paradise have, indeed, been unnaturally large over the past several decades.

Has the fish community changed over the same period?

The quality of information on changes in the fish community of Cootes Paradise has varied. Retrospective sources that document relative abundances include the commercial fishing records of the Canada Department of Marine and Fisheries (1905–1912) and Ontario Ministry of Natural Resources (1973, 1976) (and predecessors), other records of government (e.g., Kerr and Kerr 1860–1898, Royal Botanical Gardens 1950–1956), occasional scientific reports (e.g., Kay 1949), archived nonexpert observations (e.g., Thompson 1854–1886), and personal recollections (e.g., Wilmot and Harris 1893).

The taxonomic composition of the fish community in Cootes Paradise and in adjacent Hamilton Harbour unquestionably experienced profound changes over the longer term (Whillans 1979; Holmes and Whillans 1984; Holmes 1988). In the diverse early historical fish community, percids, centrarchids, and esocids were abundant. Common carp (*Cyprinus carpio*), an exotic species arriving in the late 1800s, was abundant by 1910 (Fig. 2). In the 1940s and 1950s, carp were particularly numerous and were thought to be disturbing wild rice (*Zizania aquatica*) (Lamoureux 1958). The fish community was still diverse in 1950s. By the 1970s, the fish community of Cootes Paradise was dominated by carp. Recent surveys have shown that carp and clupeids remain dominant in the fish community (Randall et al. 1993). Many marshes in other locations in the lower Great Lakes support both abundant carp and diverse marsh vegetation (e.g., Minns et al. 1993; Randall et al. 1993).

Have fish community or habitat changes occurred concurrently with intensification of natural or cultural stress?

Five types of stress have been identified in the Great Lakes in the context of aquatic ecological rehabilitation (Francis et al. 1979): natural geologic–climatic, chemical–physical loading, morphometric restructuring, exotic biota, and harvesting of biota.

The most prominent natural geologic–climatic stress in Cootes Paradise has been water level fluctuation. There and in other Great Lakes urban marshes, such as at Oshawa, Ont., on Lake Ontario and Green Bay, Wis., on Lake Michigan, periods

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of high water levels within the past 20–30 yr have been shown to coincide with the declines in wetland area, but little of the expected recovery has occurred during low water levels (Harris et al. 1981; Whillans 1982). Most of the variation in water levels is natural, although in Lake Ontario the magnitudes of the extreme highs and lows have been reduced by an outlet dam (International Great Lakes Diversions and Consumptive Uses Study Board 1981). Complicating the water level situation in the long term has been a gradual increase in water levels because isostatic rebound is tilting the Lake Ontario basin westward (Rodgers 1992*a*).

Morphometric restructuring around Cootes Paradise has been minor, as evident on aerial photographs, because the marsh has been owned and protected by the Royal Botanical Gardens. The most severe actions involved the aforementioned creation of the new outlet from the marsh and dredging of a canal. They predated the major documented changes in marsh fish and vegetational community by over 100 yr.

Harvesting of fish occurred historically. Some records of the commercial harvests are archived, as previously noted. The most intensive harvests were not very intensive and had subsided by the 1950s, again in advance of the last major transformation of the fish community (Whillans 1979).

A number of exotic fish species have invaded Cootes Paradise and (or) become relatively more numerous over the past 30 yr. Of these, only the carp has a reputation for damaging marshes. It is accused of consuming vegetation (King and Hunt 1967), uprooting vegetation (Crivelli 1983), and reducing light penetration to vegetation by resuspending sediments (Crowder and Painter 1991).

Although the adjacent Hamilton Harbour is notorious for persistent chemical contamination (Rodgers 1992*b*), Cootes Paradise is not. The surface sediments, except to a minor degree in the immediate vicinity of two outfalls, are not polluted by persistent contaminants (Rodgers 1992*a*). Nutrients are loaded via the sewage treatment plant at the west end of the marsh and are resuspended from bottom sediments but without pronounced algal contribution to the seston except at the plant outfall (Painter et al. 1989; Sager 1995). Nutrient levels are relatively high in both the sediments and water column (Painter et al. 1989) and are clearly not limiting factors for vegetation at the moment. Sediment is loaded at the relatively high rate of 1800–3000 $kg^{-1} \cdot km^{-2} \cdot yr^{-1}$ (Smith 1995) and resuspension of the predominantly fine sediments is widespread.

This summary appears in part in the recommendations of a group of experts convened by the Royal Botanical Gardens (Johnson 1990) and the background documents to Remedial Action Plan (Remedial Action Planning Team 1989). As a selection of the more obvious hypotheses about the cause of the present condition of Cootes Paradise, it focuses attention on water levels, carp, sediment loading, and suspended sediments. The summary also suggests that once one of these primary causes has been remedied, a secondary problem could emerge. For example, if the amount of suspended sediments is reduced, then light attenuation might become less limiting to plant growth than nutrient availability.

If the marsh conditions changed over time, was this related more to the intensification of stress or the failure to recover after the amelioration of stress?

This question is fundamental from a rehabilitative perspective. It is necessary to know whether or not (*i*) any of the stressors that originally caused degradation are still operative (e.g., water level is high); (*ii*) degradation occurred because the natural resilience was simply overpowered (e.g., seed bank destroyed); and (*iii*) natural resilience is latent (e.g., seed bank exists, but conditions for germination are poor). If all three are found to be true, then rehabilitative intervention should mitigate the impact of the original stressors. In fact, any case of (*i*) being true could justify this response. If only (*ii*) and (*iii*) are true, then waiting for natural correction or enhancing natural resilience would be appropriate. Any case of (*iii*) being false would require an intervention that would replace or reactivate an essential ecological function.

The studies of Portt et al. (1991) indicate that emergent marsh area in Cootes Paradise was reduced with each successive high water period. Moreover, reduction of the area of emergent vegetation during high water periods is normal in the Great Lakes. Lake Ontario last experienced high mean annual water level in the early 1980s. Thus, high water levels should not be a concern if Cootes Paradise was functioning naturally and, regardless, have not existed there for years. The absolute area of emergent vegetation that disappeared during high water levels gradually declined from the early 1970s through the 1980s. The problem with respect to emergent vegetation has not been one of increasing magnitude of area lost; rather, it has been one of incomplete recovery after each high water level period.

Inorganic turbidity has been suspected of inhibiting recovery of both submersed and emergent aquatic vegetation. Sager (1995) showed that turbidity is indeed mostly inorganic in Cootes Paradise. Sediment load and sediment resuspension are related, because much of the urban-derived sediment load is in the form of fine particles (Smith 1995). These fine sediments increase turbidity and are widely distributed in Cootes Paradise (Painter et al. 1989). Sager (1995) used exclosures in four north shore Lake Ontario marshes with different levels of turbidity (one in Hamilton Harbour and one in Cootes Paradise) to show that the turbidity inhibits the germination and growth of submersed aquatic plants. Carp and turbidity from carp activities were excluded. Similarly, Painter (1990) demonstrated, by modelling, the limitation that water clarity has on submersed vegetation in Cootes Paradise. Sagar (1995) also showed that fetch is an important determinant of turbidity. In the past, fetch was interrupted by stands of emergent vegetation. Current information does not enable distinction between the relative contributions to turbidity of anthropogenic fine sediments, exotic carp, and lengthened fetch.

An important component of resilience in marshes is the propagule bank, seeds affording resilience over the longest term. Using 20 sediment cores from each of three relatively undisturbed Lake Ontario north shore marshes, Westcott et al. (1996) found average seed densities of submersed macrophytes to be 19 273 $seeds \cdot m^{-2}$. In three comparable but disturbed marshes, including Cootes Paradise, there was little evidence of a seed bank for submersed aquatic plants that could be reactivated by the improvement of environmental conditions. Sager (1995) investigated this further by germinating a transplanted seed bank in controlled conditions in the marsh, verifying that this key recovery mechanism is incapacitated.

Evidence, thus, supports the hypothesis that the long-term

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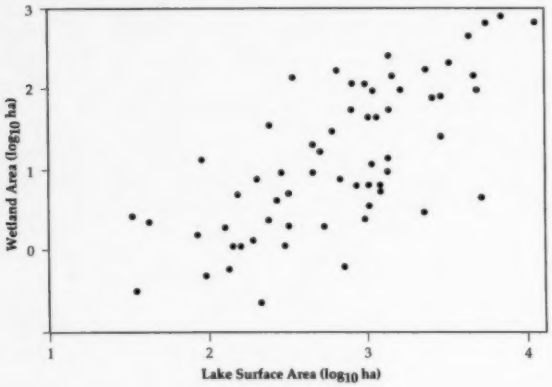
Fig. 3. The relationship between lake surface area and wetland area in 62 lakes of south-central Ontario. Areas were determined from aerial photographs using a polar compensating planimeter.



degradation of the marsh at Cootes Paradise has resulted more from the failure of recovery mechanisms than it has from the exceptional intensity of externally imposed stresses. Thus, recovery should not be expected soon without rehabilitative intervention.

What processes seem to be limiting ecological recovery?

Based on the above analysis, at Cootes Paradise attention might be devoted to rehabilitation of successional mechanisms of aquatic vegetation. Secondary succession is a natural process of recovery that, if operating, would constitute a self-regulatory capability on the part of the wetland and a basis for low intensity management. Rehabilitation could involve the following:

(*i*) Restocking the propagule bank. Reoccupation of the marsh by aquatic plants might occur naturally over time, but a long time. Transplantation would be advisable in erosive sites, in locations where the aerial portion of plants once interrupted fetch and where the most extensive stands existed historically. Fetch-breaking robust emergents such as cattail (*Typha*) or burreed (*Sparganium*) would need to be transplanted, the roots of which would stabilize sediments. Seed banks or propagules of submerged vegetation would also be reintroduced in the shallower locations (less limited by light) where submersed plants dominated historically.

(*ii*) Reduction of fetch and stabilization of sediments. Transplantation of the large conservative stands of emergent vegetation that serve these functions would help, but the historical substrate and morphometry have been modified such that survival of the plants would be difficult. Therefore, construction of low profile islands, "hard points," with new detrital substrate and gradual slopes for transplants would also be useful.

(*iii*) Temporary exclusion of carp. Evidence implicates carp in inhibiting recovery of aquatic plants, not as causes of loss. Thus, barriers to temporarily exclude carp would allow the re-establishment of the relatively large stands of aquatic vegetation that could coexist with carp.

(*iv*) Reduction of sediment load in the watershed. This longer term tactic would involve both changing agricultural or construction practices and mitigating the effects of such uses through techniques such as buffer vegetation and settling ponds. These techniques are conventionally understood but difficult to implement because many land owners are involved and because the space required is at a premium in the heavily settled watershed of Cootes Paradise. Retrospective or comparative assessment could provide sediment budget targets but would not guide the reprioritization of actions that would achieve them.

A need-by-need sequence of intervention, monitoring, and adjustment of priorities could not be expected to solve the sediment problem expediently. In a complex multistress situation with large time lags needed to detect watershed-scale response to intervention, expedient restoration would likely require a strategy of concerted action on all major sediment sources in the watershed. Given the long-term deepening of Cootes Paradise through isostatic rebound, reduced inputs of fine sediment, although improving water clarity, could hasten the deepening of the marsh and the dominance by deeper living vegetation.

What would constitute full rehabilitation?

Quantitative targets would be useful to evaluate that rehabilitation has occurred. Retrospective assessment indicates that complete restoration of vegetation in Cootes Paradise to cover the area that was vegetated in the late 1800s would require regeneration of 213 ha, while maintaining the 37 ha of vegetated marsh that remains. Replacement of the historic marsh area of Hamilton Harbour and Cootes Paradise combined would require a target of 420 ha. These figures, based on historic maps (Whillans 1982), refer to the area circumscribed by emergent vegetation, but not occupied exclusively by emergent plants. A target of 420 ha would be unreasonable, because the harbour facilities cover almost 40% of the historic marsh.

How does the 213-ha target compare with what would be considered normal for a water body of the size of Cootes Paradise and Hamilton Harbour? Figure 3 shows the relationship between wetland area and lake surface area for 66 lakes in south-central Ontario ($r^2 = 0.64$, $p < 0.05$). Wetland area ranges from almost 0% to 38% of the area of the lakes. The average is 4.2%. If this proportion is used as a rehabilitation target for the 2350 ha Hamilton Harbour and Cootes Paradise (Rodgers 1992*b*), about 99 ha of wetland should be rehabilitated.

Alternatively, Inskip (1982) proposed a model for estimating the area of habitat required by northern pike (*Esox lucius*). Anderson (1993) expanded the model to estimate reproductive habitat suitability in terms of the type and density of vegetation and then applied it to Hamilton Harbour. The target would be approximately 18 ha. If the area of Cootes Paradise is included with that of the harbour, then 20 ha would be required.

The goal based on the average wetland area for a lake the size of Hamilton Harbour and Cootes Paradise (99 ha) discounts the inherent value of the former wetlands and the as yet unquantified value of the wetlands in this location for the rest of Lake Ontario. It does suggest that, to the degree that wetlands serve adjacent open-water areas ecologically, full restoration of the former wetlands would not be necessary to reasonably assure the recovery of those immediate open water areas. Finally, there is the implication that recovery of functions such as habitat for fish spawning might require even smaller areas of specific types of wetland.

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What ecological components should be monitored to facilitate future retrospection?

A test of sustainability is persistence. Accountable development will involve the monitoring of persistence, in fact enabling retrospection. The components that should be monitored include the following.

(*i*) Components for which long-term data series already exist. Tilman (1989) for ecology in general and Smol (1995) for aquatic ecology document that long-term (longer than 3–5 yr) data series are rarely used. Long-term data series on fish (25 yr would be multigenerational for most freshwater fish species) and their habitat are uncommon but valuable (Whillans et al. 1990). Their longevity indicates that they have repeatedly proven to be useful. They should be continued unless found to be meaningless. Use of data series for purposes not originally intended could require as much work on calibration data sets (Smol and Glew 1992) as the primary data series.

(*ii*) Components that are useful indicators of ecological state. Freedman et al. (1993) summarized such indicators. Closely related are indicators of ecosystem health (Smol 1995) and ecosystem integrity (Keddy et al. 1993). Indicators would reflect both the level of stress (positive and negative) experienced by the marsh and the resilience; what should be monitored would vary from situation to situation. For Cootes Paradise, high stress levels might be reflected in high turbidity, dominance of cattail or carp, reproductive failure of northern pike, no succession, shift in the concentration of stored energy from pelagic to detrital organisms, and ratio of endemic to exotic species abundance. Resilience might be indicated through seed bank diversity, preadaptation of vegetation to water level regime, and proximity of biotic refugia such as gradually sloped vegetated shorelines along which plants could migrate in response to water level change.

(*iii*) Components such as sport fish that are valuable to the people who are interested in the rehabilitation (Munn 1993). In contrast to the monitoring of indicators, the techniques for monitoring these components are conventional, though not often applied over the long term.

Narrative science: retrospective and comparative contributions

Lee (1993) used the adaptive environmental management idea of Holling (1978) to argue that intervention in ecological systems is not a science where the outcome is predictable. The science of intervening in complex systems is an experimental process in which heuristic models offer more integrative guidance than predictive models. It is narrative science that informs judgement about which actions to take simultaneously to mitigate limiting factors. Careful monitoring of the system response will provide important, but often ambiguous information about why the intervention was or was not successful, allowing the revision of the narrative. The narrative is, thus, a macro-hypothesis, untestable as a whole, but testable in part. The narrative is a synthesis that earns acceptance in the scientific community based on its logical strength and the community's perception of the experience or information base of the narrator. Simultaneous action on multiple factors has a chance of achieving the desired environmental end, whereas a factor-by-factor approach would fail or be impractical because factors are too interdependent, the response times are too long, and the factors are likely to change after each intervention. More important, the success of the particular intervention in terms of specific habitat conditions is rendered less critical than the ability to explain the outcome and to avoid repeating errors in future interventions in similar circumstances.

Table 1 shows that at each stage in the development of the narrative science for the rehabilitation of aquatic vegetation in Cootes Paradise, retrospective and comparative work resulted in imperfect data bases that necessitated assumptions about ecological processes and condition. The narrative science was developed deductively and heuristically by iterating between retrospective and comparative investigations. The comparative work provided evidence on ecological process that would have been difficult to obtain retrospectively. Experimentation was used to test assumptions about processes and to inductively formulate others.

The process of marsh degradation and recovery were asymmetrical, as were the inquiry processes about curtailing degradation and undertaking rehabilitation. However, some approaches were shared. In the future, retrospection will become less important as a source of new information to guide the rehabilitation of Cootes Paradise than will comparison and experimentation, although the knowledge base of past retrospection will continue to be important for reference when verifying rehabilitation. The recent state of the marsh ecosystem is relatively unprecedented locally; thus, understanding the responses of individual components to intervention can be improved by probing or stimulating them or by detailed comparative study.

The Cootes Paradise rehabilitative experience has involved the undertaking and planning of large-scale, multiple-tactic interventions that could be monitored and adjusted according to systemic responses that are cumulative in nature. The narrative science that is the basis for the intervention is, thus, a form of assessment of cumulative effects. Bedford (1990) argued that the assessment of wetland cumulative effects depends heavily upon the understanding of geographic (spatial) and historical (time series) context. At the regional scale, overlay-type analysis can contribute to this understanding (Johnston 1994). The implication of the Cootes Paradise situation is that, for complex site-specific rehabilitative processes, narrative science enables understanding of cumulative effects to be used as a basis for rehabilitative intervention in advance of, or without, understanding the effects of individual stressors.

This rationalization of narrative science neither defends "shotgun" (random, multiple intervention) rehabilitation, nor does it address efficiency of rehabilitation. The aforementioned work by Anderson (1993) on reproductive habitat needs of northern pike in Cootes Paradise and Hamilton Harbour indicates that a functional assessment could reduce the estimated area that needs to be rehabilitated from 99 to 20 ha. Bedford's (1990) point is well taken that clear goals should be established initially. Clear goals for wetland fish habitat in Great Lakes marshes that support, say, 30–60 resident or transitory fish species would not be easily prioritized in a multiple use situation and when the ecological information base is weak for the majority of the species. Narrative scientific synthesis using representative species and habitats and assumptions about causes and effects will likely prevail for some time.

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Table 1. Narrative sequence and sources of supporting evidence for the rehabilitation of Cootes Paradise aquatic vegetation.

Narrative component	Evidence
	Problem identification
Natural pulse stability of Cootes Paradise	Retrospective: Historical maps, aerial photos and field observations Limitations: discontinuous; bias for emergent vegetation and the last 50 yrs Comparative: historical maps, aerial photos, field observations, and sediment cores from marshes in Lakes Ontario, Erie, and Michigan Limitations: bias for emergent vegetation; the marshes have different topographic settings; few coring sites
Vegetation disappeared during high water levels, but did not recover during lows	Retrospective: aerial photos and water level data series Limitations: discontinuous: bias for emergent vegetation and the last 50 yr Comparative: reports from other Great Lakes locations Limitations: dates of aerial photo do not align with the dates of peak water levels
	Factors causing vegetational change
High turbidity prevents vegetational recovery	Retrospective: historical field observations on turbidity Limitations: short-term data series Comparative: synoptic survey of marsh plants along the north shore of Lake Ontario in a range of turbidities Limitations: original plant communities unknown; field levels of turbidity are highly variable in time Experimental: turbidity levels in turbidity exclosures; response of transplants in exclosures; germination and growth in light limited growth chambers Limitations: artificial conditions alter more than turbidity and inhibit synergisms
Seed bank is impoverished	Retrospective: seed counts in sediment cores Limitations: natural seed bank unknown Comparative: seed counts in sediment cores in well vegetated marshes Limitations: source of seeds and their relative importance is unknown Experimental: transfer seed bank into exclosures in Cootes Paradise Limitations: the seeds may not be for locally adapted plants
Carp prevent regeneration of vegetation	Retrospective: historic observations of carp abundance Limitations: relationship of carp abundance to vegetational community is conjectural Comparative: observations of carp abundance in north shore Lake Ontario marshes and elsewhere in the Great Lakes with and without vegetational regeneration Limitations: the number of quantified marshes is small, thus generalization is difficult Experimental: radio-tracking of carp around vegetation; germinate and grow plants in carp exclosures Limitations: tracking shows only carp location; carp can influence plants indirectly by silt resuspension through exclosures
Sediment cores show rate of sedimentation and particle size	Limitations: most sediments are not stable enough for precise estimations Experimental: sediment budgets created Limitations: sediment sources are untraced
Fetch and related turbidity have increased because emergents have disappeared	Retrospective: historic aerial photos Limitations: turbidity records are limited for periods of photos Experimental: transplants in turbidity exclosures Limitations: turbidity exclosures do not perform the same as emergent stands
	Factors relevant to rehabilitation
Carp must be excluded for revegetation	Experimental: use small exclosures for transplants Limitations: other influences are also excluded
Vegetation or seed banks will have to be transplanted at times during rehabilitation	Comparative : transplant to marshes representing a range of conditions Limitations: small scale transplants will differ from large scale in survival; the range of conditions may not include extremes such as high water levels Experimental evidence: transplant using a range of site preparation Limitations: only short-term response is seen

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Table 1 *(concluded).*

Narrative component	Evidence
Fetch should be interrupted	Comparative: measurements of fetch in other marshes that have retained resilience Limitations: fetch might have a different effect early in the rehabilitation process Experimental evidence: transplant behind small-scale barriers to fetch Limitations: small-scale barriers cannot mimic all fetch situations; not only fetch will be effected
Fine sediment input must be controlled over the long term	Experimental: simulate sediment budgets with and without fine sediments Limitations: budgets do not account for sediment distribution; coarse sediment influences and effects on water depth are difficult to isolate
Turbidity must be temporarily excluded	Experimental: control turbidity in growth chamber, greenhouse, and field exclosure transplants Limitations: more than turbidity is controlled

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The linkage among ecosystem perturbations, remediation, and the success of the Nipigon Bay fishery

John R.M. Kelso and Ken I. Cullis

Abstract: Since the inception of the commercial fishery in Nipigon Bay of Lake Superior, walleye (*Stizostedion vitreum*) and lake sturgeon (*Acipenser fulvescens*) have been extirpated and the abundance of lake trout (*Salvelinus namaycush*), brook trout (*Salvelinus fontinalis*), and northern pike (*Esox lucius*) has declined significantly while the abundance of lake whitefish (*Coregonus clupeaformis*) and lake herring (*Coregonus artedii*) has increased. Systemic stresses including eutrophication, airborne contribution of contaminants, and exploitation (reduced by closure of the commercial fishery in 1988) remain but may not impair populations of lake whitefish and herring, which interact less with tributaries and nearshore waters. Improvements in habitat, through water flow management in the Nipigon River, removal of logs in the nearshore, shoreline and stream restoration, cessation of log drives, as well as artificially increasing adult abundance have resulted in resumption of some limited reproduction by walleye and increased egg deposition and early life survival by brook trout. Multiple stresses are still ubiquitous in the Nipigon ecosystem, but relief of several stresses in tributaries and nearshore environments at least appears to have resulted in an initially encouraging response by two species dependent upon these areas.

Résumé : Depuis les débuts de la pêche commerciale dans la baie Nipigon du lac Supérieur, le doré jaune et l'esturgeon jaune sont disparus de cette baie, et on a observé une diminution appréciable de l'abondance du touladi, de l'omble de fontaine et du grand brochet. Par contre, le grand corégone et le cisco de lac sont devenus plus abondants. Les sources systémiques de stress, comme l'eutrophisation, les retombées atmosphériques de polluants et l'exploitation (facteur de moindre importance depuis la fermeture de la pêche commerciale, en 1988), sont toujours présentes mais ne nuisent peut-être pas aux populations de grand corégone et de cisco de lac, dont l'interaction est moindre avec les tributaires et les eaux côtières. Les améliorations apportées aux habitats (gestion du débit de la rivière Nipigon, enlèvement des billes près des côtes, restauration des berges et des petits cours d'eau et cessation du flottage des billes) ainsi que l'augmentation artificielle de l'abondance des adultes ont permis une reprise limitée de la fraye chez le doré jaune ainsi qu'une ponte accrue et un meilleur taux de survie juvénile chez l'omble de fontaine. De nombreuses sources de stress sont encore omniprésentes dans l'écosystème de la baie Nipigon, mais il semble à tout le moins que l'atténuation de plusieurs sources de stress dans les tributaires et les milieux riverains a donné des résultats encourageants en ce qui concerne deux espèces dépendant de ces habitats.
[Traduit par la Rédaction]

Introduction

Salmonines and coregonines have been the mainstay of the sport, commercial, and subsistence fisheries in Lake Superior and its tributaries since early settlement of the Lake Superior basin by Europeans. Percids and brook trout (*Salvelinus fontinalis*) also formed important localized sport and commercial fisheries in Nipigon Bay (Ryder 1968; Schneider and Leach 1977; Colby et al. 1991). Since the earliest days of European exploration and settlement, whitefish (*Coregonus sp.*) have been sought after and acclaimed throughout Lake Superior (Goodier 1982), and Nipigon Bay was no exception (Millard 1917[2]; Hewitt 1948). When lake trout (*Salvelinus namaycush*) stocks declined in Nipigon Bay, attention turned to lake herring (*Coregonus artedii*), walleye (*Stizostedion vitreum vitreum*), and yellow perch (*Perca flavescens*). Unlike other Great Lakes areas, the late 19th century development of tourism, which focused upon the renowned brook trout sport fishery in Nipigon Bay (Whitcher 1888; Millard 1917, see footnote 2), was locally significant until this fishery too became depleted. The commercial walleye fishery in Nipigon Bay was second only to that in Black Bay in Lake Superior and a walleye sport fishery also was important to the local Nipigon Bay economy. Walleye were extirpated in the 1960s (Ryder 1968).

In 1986, Nipigon Bay was identified as one of 17 areas in Canadian waters of the Great Lakes where water quality or beneficial uses identified under the Great Lakes Water Quality Agreement (1987) were impacted. A Remedial Action Plan (RAP) has been under development to both restore beneficial uses of the ecosystem and reduce the causes of impairment.

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[2] Millard, E.E. 1917. Days on the Nepigon. Unpublished manuscript.

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These plans for remediation post-dated almost a century of man-made perturbations but also man's efforts to enhance and protect Nipigon Bay fisheries, some species of which were assumed to be isolated stocks (Ryder 1968). If society is to achieve the management objectives defined by the Great Lakes Fisheries Commission (Busiahn 1990) and International Joint Commission (IJC) remediation plans (RAP 1991[3]) for Great Lakes, managers must utilize initiatives or approaches shown to have potential by experience gained from past application. Herein, we review available data for the Nipigon Bay fishery, evaluating possible causes of changes to the fish community and evaluating benefits from stocking, habitat enhancement, and contaminant reduction in Nipigon Bay, so that other managers may benefit from the Nipigon Bay experience.

The Nipigon area

The Nipigon River, the largest tributary of Lake Superior, flows south for some 50 km from Lake Nipigon to Lake Superior (Fig. 1) through a gorge following a geological fault (Near 1982). The river delivers a mean annual flow of approximately 370 $m^3 \cdot s^{-1}$ (Kelso et al. 1977). Elevation drops 75 m, and at one time, falls and rapids comprised approximately 16 km of the river's route. The river now supports three hydroelectric installations and has lakes that alternate with turbulent stretches. Lake Helen, the largest lake, is a natural water body and the Nipigon River flows through the southern corner of the lake, making Lake Helen available as habitat to anadromous species.

Nipigon Bay drains a watershed of almost 40 000 km^2. The bay extends about 16 km south and 40 km east from the entry of the river and features two primary channels connecting it to Lake Superior. These channels govern main directions of water flow (Polak and Palmer 1977) in Nipigon Bay.

Human population within the Lake Superior basin doubled between 1880 and 1900 and between 1900 and 1960 but has remained virtually unchanged since 1960 (data from Beeton 1969; Advisory Services, Statistics Canada, Ottawa, Ont.). In keeping with slow population growth and limited industrial development, the oligotrophic upper Great Lakes have shown little environmental change since the turn of the century (Beeton 1969). Human development in Nipigon Bay is concentrated in the town of Nipigon (population ≈ 2400) and Red Rock (≈1400), and historic smaller centres (construction camps at Parmachene, Cameron Falls, and Pine Portage; logging camps at Virgin Falls, Lake Helen, and elsewhere) no longer exist (Wilson 1990; RAP 1991, see footnote 3; Kelso and Demers 1993).

Chemical changes in the aquatic system

Algal blooms or "abundant" growths of epiphytic algae were evident in parts of the lower Nipigon River in the early 1950s (Ontario Ministry of Natural Resources (OMNR) files, Nipigon District), the late 1960s (OMNR files, Nipigon District) and in the 1980s (R.A. Ryder, personal communication). However, those effects of cultural enrichment, which were localized and did not result in systemic eutrophication (Minns 1977; Kelso et al. 1977), are apparently declining and are unlikely to significantly affect the ecosystem (RAP 1991, see footnote 3). An inadequate communal septic system at Red Rock was replaced in 1978 by a primary treatment plant and the small treatment plant at Nipigon was replaced in 1976 by a primary treatment plant that doubled capacity.

Ecosystem perturbation from the Domtar Red Rock Pulp and Paper Mill, was first recognized by German (1968) and Ryder (1968), and was the focus of an interdisciplinary study in the mid-1970s (*Journal of the Fisheries Research Board of Canada* 34(6), 1977). The mill effluent induced taste and odours in fish flesh (German 1968; Whittle and Flood 1977), affected biotic community structure (Ryder 1968; Kelso 1977; Rokosh et al. 1977; VanderWal 1977), affected production (Moore and Love 1977; Whittle and Flood 1977; Cooley 1977; Leslie and Kelso 1977), altered substrates (Johnson 1977; Sandilands 1977), and resulted in the accumulation of contaminant burdens in fish (Kaiser 1977; Kirby 1986; Suns et al. 1991). The chemical quality of the mill effluent has improved since 1970, but while taste and odour problems in fish no longer exist, in 1990 the 96-h LC50 to rainbow trout (*Oncorhynchus mykiss*) ranged between 44 and 100% dilution of the raw effluent, similar to that found by Whittle and Flood (1977). More recent (1992–1995) process changes, including the closure of the bleach plant and conversion of the newsprint machine to linerboard, has eliminated loadings of chlorinated organic compounds and further reduced the effluent toxicity and biological oxygen demand. Installation of a secondary (extended aeration) effluent treatment system, scheduled for completion by December 31, 1995, should result in a nontoxic effluent. There are currently no restrictions on the consumption of fish as food, and no apparent deformities or reproductive problems in wildfowl occur that can be attributed to the mill effluent (RAP 1991, see footnote 3; Nipigon Bay RAP Team 1994[4]). The mill still withdraws and discharges 95 000 m^3 day^{-1} of Nipigon Bay water and macroinvertebrate community characteristics are related to distance from the outfall.

An additional chemical stress to the aquatic system may have been deliberate applications of pesticides in Nipigon Bay watersheds (Fig. 2). The insecticide DDT was applied directly to streams for the control of blackfly (*Simulium* spp.) larvae in the 1950s and 1960s (German 1968) and over an unknown but extensive land area for control of spruce budworm (*Zeiraphera canadensis*) (HEPC 1945; Gollat 1975). Applications to effect blackfly control were likely concentrated near the hydroelectric construction towns of Pine Portage (population up to 2000) and Cameron Falls (population up to 2800) during the 1950s and 1960s. Use of DDT ceased by 1970. Postupalsky (1970) suggested that eggshell thinning and reproductive problems in double-creasted cormorants (*Phalacrocorax auritus*) and bald eagles (*Haliaeetus leucocephalus*) in Nipigon Bay might have been attributable to DDE in the past. Currently, body burdens of contaminants in fish do not exceed public health guidelines for consumption by the public (RAP 1991, see footnote 3); few past tissue analyses (German 1968; Kaiser 1977) exceeded current guidelines. Information on body burdens of contaminants in wildlife is scarce; however, levels of organochlorines (including DDT) sampled in egg

[3] RAP. 1991. Nipigon Bay: environmental concerns and issues. Stage 1 Report. Environmental conditions and problem definition. Unpublished report.

[4] Nipigon Bay Rap Team. 1994. A discussion of remedial options in the Nipigon Bay area. Unpublished report.

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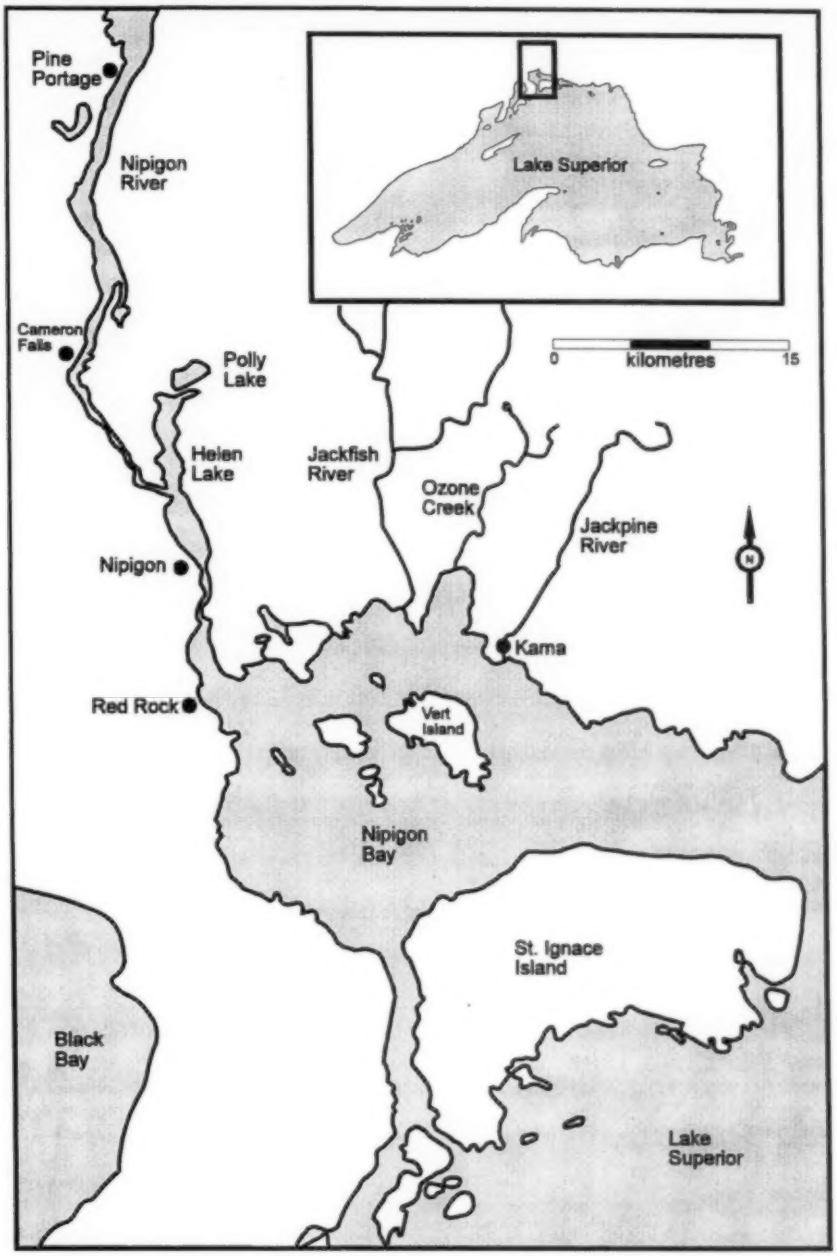
Fig. 1. Nipigon Bay and Nipigon River in Lake Superior.



shells of herring gulls (*Larus argentatus*) and double-crested cormorants from the Nipigon Bay area have steadily declined since the early 1970s (Nipigon Bay RAP Team 1994, see footnote 3). Populations of bald eagles and double-crested cormorants have experienced a concurrent increase in abundance during this time (Bryan 1991; Escott and Bryan 1993) indicating that past DDT levels may have impacted populations. However, it is not clear if impacts on fish were present.

Physical changes to the aquatic system

The first significant changes to aquatic physical habitat were likely to accommodate the first, established in 1717, of the posts by the (North West and Hudson Bay Company) fur trading companies through the modification of the lower river to accommodate shipping (Wilson 1990; Kelso and Demers 1993). By 1820, the Nipigon River trading posts were central

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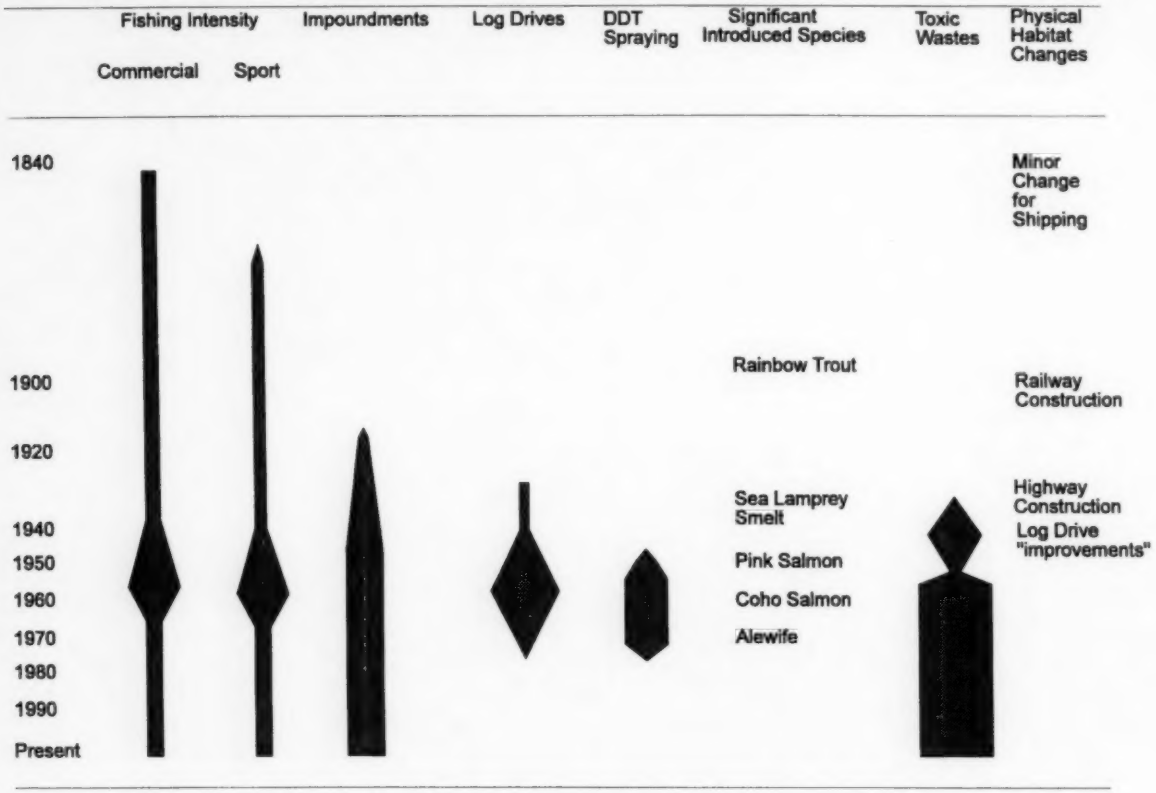
Fig. 2. Chronology of change affecting the Nipigon Bay ecosystem. Width of the time line indicates relative degree.



to traders travelling both west and north (Dawson 1969). Red Rock House, at the mouth of the river, was an important Great Lakes transhipment point for furs and supplies in the 1880s.

The construction of the Lake Superior section of the Canadian Pacific Railway (CPR) began, in the early 1880s, the period of the most dramatic changes to the physical characteristics of the Nipigon River and Nipigon Bay. Construction of kilometers of roadbed along Lake Superior shores and Nipigon River embankments, dredging of the estuary and river channel to facilitate upstream ship passage and construction of piers and pilings all affected the waterway (MacCallum 1990; Wilson 1990; Kelso and Demers 1993). The CPR, the Nipigon River Tramway (now defunct), and the National Transcontinental (now the Canadian National Railroad) all traversed area tributaries, modified shorelines, and affected both morphometry and changed river and nearshore substrates by introducing material. It is possible that the walleye spawning area in the lower river first identified by Ryder (1968) was actually created during construction of the CPR bridge in 1884 (Kelso and Demers 1993) by the addition of fill material.

The hydroelectric power potential of the 95-m difference in elevation (Bell 1870) between the Nipigon River headwaters at Red Rock House and Lake Nipigon itself was first exploited by the dam at Cameron Falls in 1920. Three sites (Pine Portage (1950), Cameron Falls (last unit 1926), and Alexander Falls (last unit 1945; Fig. 1) currently produce approximately 170 000 kW of energy. In 1943, the diversion of the Ogoki River from the Hudson Bay to the Great Lakes drainage system was completed, increasing river flow by about 30%. Construction of hydroelectric facilities from 1920 to 1950 blocked fish immigration to the upper river, permanently flooded historic rapids, and forever altered the morphometry of lakes in the river system (Figs. 2 and 3).

The log drives between 1938 and 1972 resulted in between 20 000 and 420 000 cords (570 – 12 000 m^3) passing annually through the Nipigon River (Fig. 4). Log drives may have begun as early as 1911 (Kelso and Demers 1993) and, almost certainly, occurred annually for some length of the river between 1923 and 1938. To facilitate log drives, "obstructions" in the river were removed; pilings, booms, and shore protectors were constructed (these were termed "improvements"); and booming areas (where logs were collected) were created in the lower river and in Nipigon Bay. Log drives and water transport of wood ceased in 1973 (Fig. 2).

A sawmill located between Nipigon and Red Rock sawed local woods for lumber and provided groundwood pulp to the Red Rock pulp mill operated between 1921 and 1953 (RAP 1991, see footnote 3). Wood handling facilities for this sawmill extended some 0.5 km into Nipigon Bay and woody debris accumulated on and near the shore.

Removal of substrate through the collection, by hand or dredge, of pebble and cobble in shipload quantities occurred

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Fig. 3. Changes in morphometry to the Nipigon River between 1921 and 1972 and to the estuary between 1935 and 1993. Many of the features identified in 1921 no longer exist today due to flooding by dam construction.

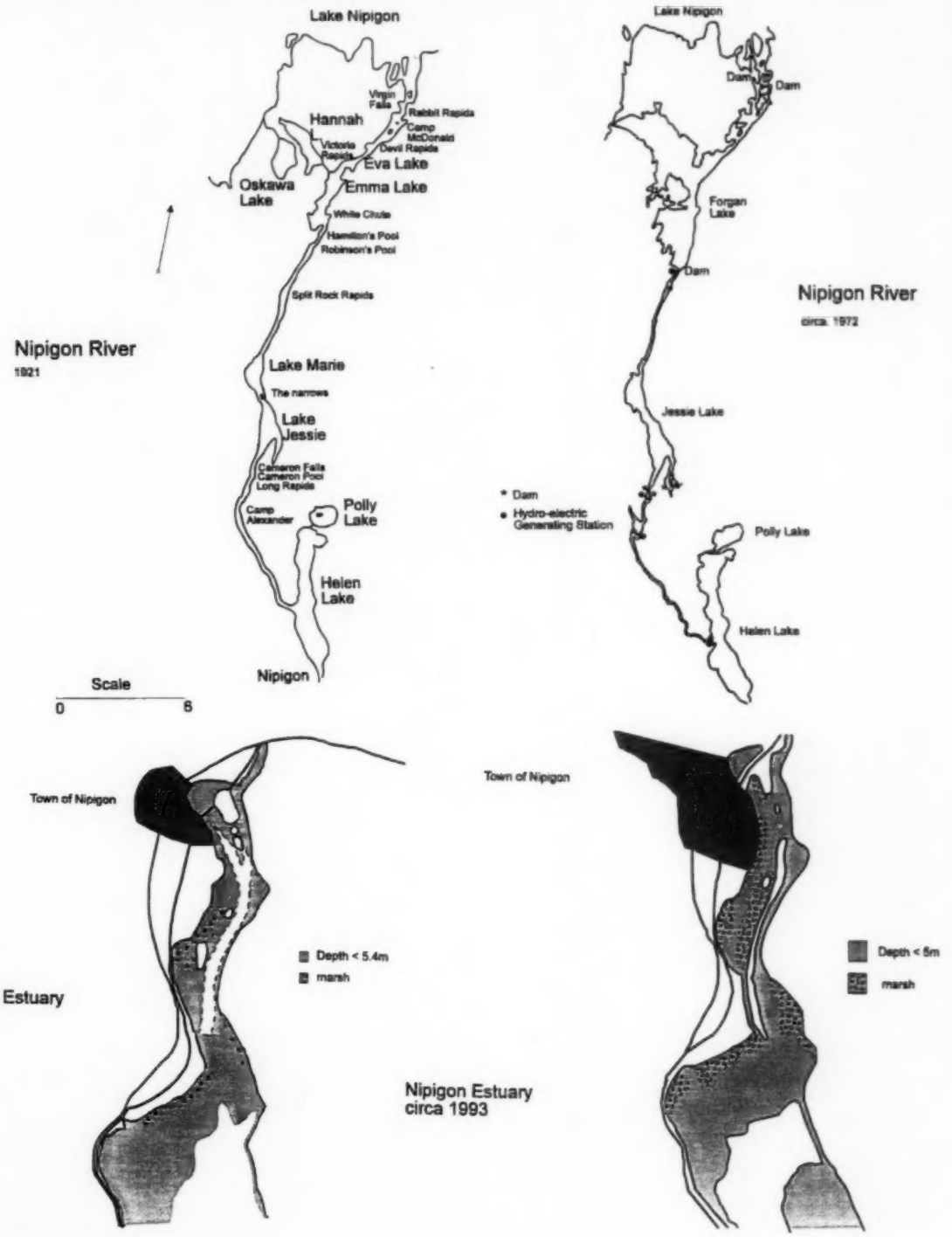

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Fig. 4. Annual volume of wood transported in log drives of the Nipigon River, 1938–1972.

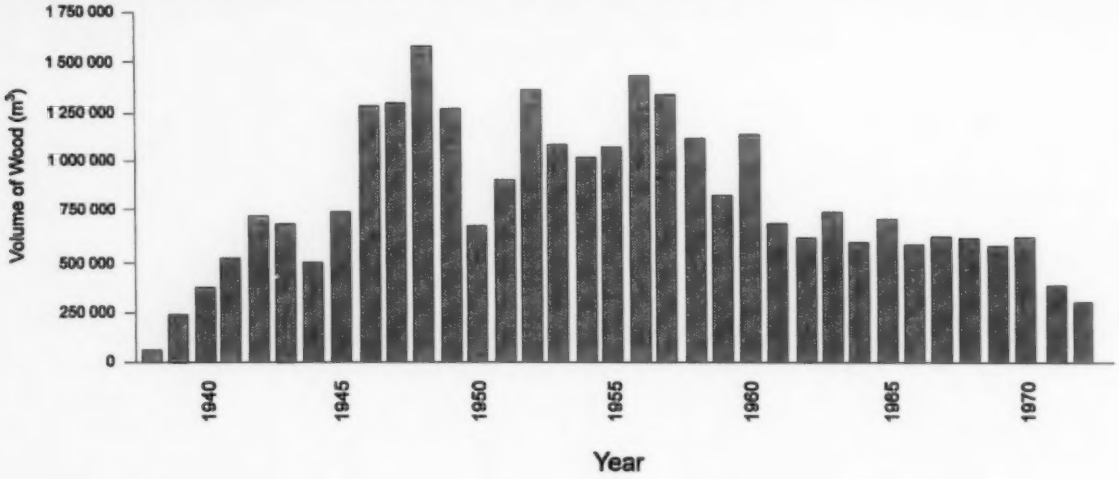
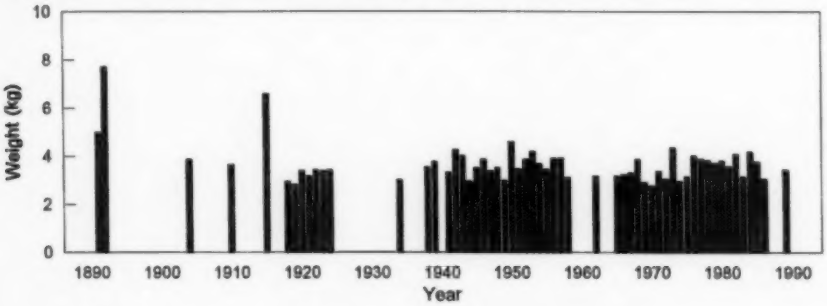


Fig. 5. Weight of the largest brook trout caught annually from the Nipigon watershed. Data are from Wilson (1990).



at nearby Jackfish (Marcella 1989) in the early 1900s. Wind and wave action conveniently sorted, cleaned, and rounded granitic materials to 50–200 mm and created an excellent material for grinding soft ores. It is probable that pebble and cobble "mining" occurred in Nipigon Bay as beach deposits of cobble are common, but no records are available.

Collectively, these changes left Nipigon Bay far from the "relatively pristine" conditions (Great Lakes Water Quality Agreement 1978, amended 1987; IJC 1992) envisaged by most for Lake Superior.

The Nipigon Bay fishery

European trappers and fur traders likely caught or traded for fish since late in the 17th century just before the first trading post was established (Dawson 1969). By 1839, the Hudson's Bay Company caught enough fish so that it might be regarded as an active commercial fishery. Red Rock was one of at least three seasonal fishing outposts (Agawa River, Batchawana Bay, Red Rock) on Lake Superior. The Red Rock posts major product was whitefish (Goodier 1982). In 1877, the fishery expanded to provide food for those working on the construction of the CPR in 1883–1885 (Goodier 1982). Whitefish was likely the preferred catch followed by lake trout.

The commencement of the sport fishery in Nipigon Bay and Nipigon River is uncertain but brook trout were sought by nonresident anglers in 1865 (Whitcher 1888). Apparently, the Nipigon area was famous even in the 1860s and anglers thought the ease of catching brook trout such that, even then, the fishery was being "ruined" because of overharvest. Steamship service in the late 1800s (Dawson 1969) and the completion of the CPR enhanced the flow of people as well as goods. No record of brook trout harvest exists, although yield is assumed to have dramatically decreased (MacCallum 1990). Maximum size reported from annual fishing derbies has remained stable since about 1920 (Fig. 5); however, only one brook trout has exceeded 4.5 kg since the world record (6.6 kg) was angled in the Nipigon River in 1915 (Scott and Crossman 1973). As a result of low abundance and to support efforts to enhance brook trout populations, brook trout have been excluded from local fishing derbies since 1994.

Walleye and lake sturgeon were regarded as "nuisance" species in the late 1800s (Wilson 1990; Goodier 1981, 1982). Walleye (and probably lake sturgeon) were removed as coarse fish (MacCallum 1990; Wilson 1990) in the late 1800s to early 1900s in an attempt to enhance brook trout populations. Ryder (1968) indicated that walleye constituted only a small portion of the catch of the three major species (whitefish and lake

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Table 1. Stocking history for the lower Nipigon River and eastern Nipigon Bay in 2-year time steps, 1920–present.

Year	Brook trout	Whitefish	Arctic grayling	Lake trout	Walleye[a]
1914	?[b]				
1920–1921	20 000[d]				
1922–1923	310 500[d]				
1924–1925	165 000[d]	2 000 000[d]		20 000[d]	
1926–1927	199 700[f]			25 000[d]	
1928–1929	90 000[d]				
1930–1931	110 000[d]				
1932–1933	346 267[f]				
1934–1935	564 000[f]				
1936–1937	56 800[d]				
1938–1939	244 640[f]				
1940–1941	55 600[d]				
1950–1951	52 400[f]			30 000[e]	
1952–1953	10 000[f]				
1954–1955	6 000[e]			5 000[d]	
1956–1957	1 500[e]				
1958–1959			990[e]		
1960–1961	100[e]				
1962–1963					
1964–1965					
1966–1967					
1968–1969				9 000[e]	
1970–1971				17 000[e]	
1972–1973				2 500[e]	
1974–1975	10 500[f]			14 500[e]	
1976–1977				14 500[e]	
1978–1979					1 378 080[e]
1980–1981					1 388 500[f]
1982–1983	1 051 438[g]			40[e]	4 622 755[f]
1984–1985	304 702[f]			597 892[d]	4 729 835[f]
1986–1987	9 000[d]			628 625	426 810[f]
1988–1989				767 401	277[e]
1990–1991					7 880[e]
1992–1993					4 254

[a]2450 adult walleye released between 1986 and 1989.
[b]Unknown (small) numbers of brook trout stocked.
[c]Egg.
[d]Fry/fingerling.
[e]≥12 months.
[f]Mixed stock.
[g]Mixed stock including 653 000 eggs distributed into the Nipigon River system.

trout) between 1945 and 1965 (Fig. 6). No walleye were captured in the commercial catch from 1967 to 1984 (Ryder 1968; Fig. 6), at which time the remaining two commercial fishing licences for Nipigon Bay were purchased by the Ontario Ministry of Natural Resources and all commercial fishing in western Nipigon Bay ceased. Currently, only a small native subsistence fishery remains on Lake Helen. The sport fishery for walleye post-dated that for brook trout and while the latter fishery was still highly regarded in the late 1930s (E.W. Mills, unpublished data)[5] the walleye fishery never achieved similar prominence for sport fishers.

[5] Mills, E.W. Paddle, pack and speckled trout. Tales of fishing in northern Ontario in the 1930s and 1940s. Unpublished manuscript.

The cumulative commercial and sport fishing efforts in Nipigon Bay comprised 15% of that in Canadian waters of Lake Superior and, with few exceptions, followed the pattern observed in Lake Superior (Fig. 6). Generally, catches of lake trout, whitefish, and herring declined from a peak in the early 1900s. Walleye catches increased to a maximum in the 1960s then precipitously declined as did walleye populations elsewhere in western Lake Superior. Brook trout catches by anglers notably declined after the 1940s (E.W. Mills, unpublished data, see footnote 5). Brook trout catches in the Nipigon River declined from a reported average afternoon catch of approximately 27 kg in the early 1880s (MacCallum 1990) to a total estimated angler harvest of 96 brook trout in 1993 (July 25 – Sept. 15) for Nipigon River and Nipigon Bay (Kushnier 1994).

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Fig. 6. Yield reported by commercial fishers from Nipigon Bay (left) and Lake Superior (right) 1875–1988. (*a*) All species; (*b*) lake whitefish; (*c*) lake herring; (*d*) lake trout; (*e*) walleye; (*f*) lake sturgeon. Data are from (●) Ford (1943), (*) Schneider and Leach (1977), (▲) Baldwin et al. (1979), (■) Goodier (1982), (◆) Wilson (1991), and (▼) OMNR (Lake Superior Unit, Thunder Bay).

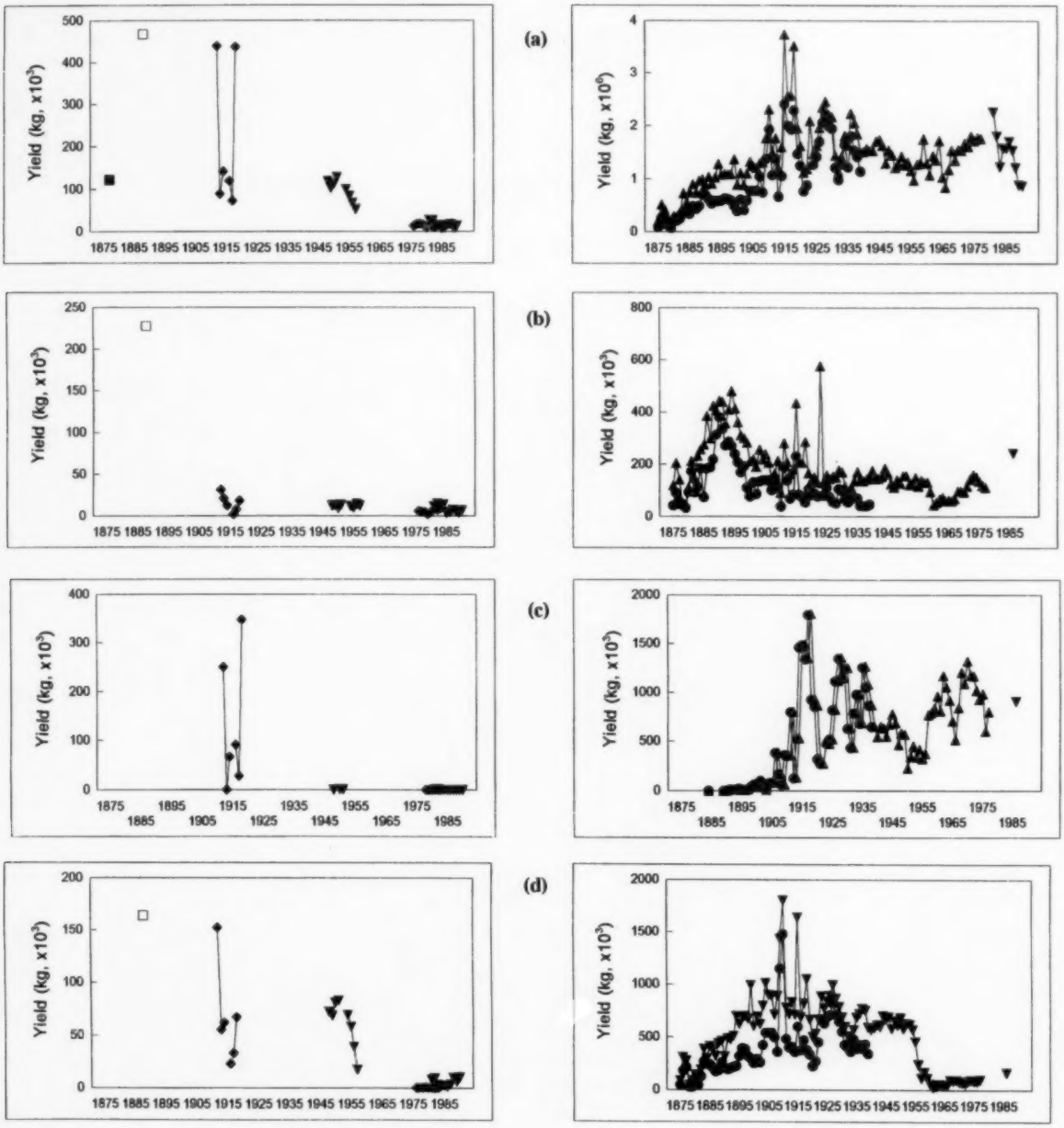

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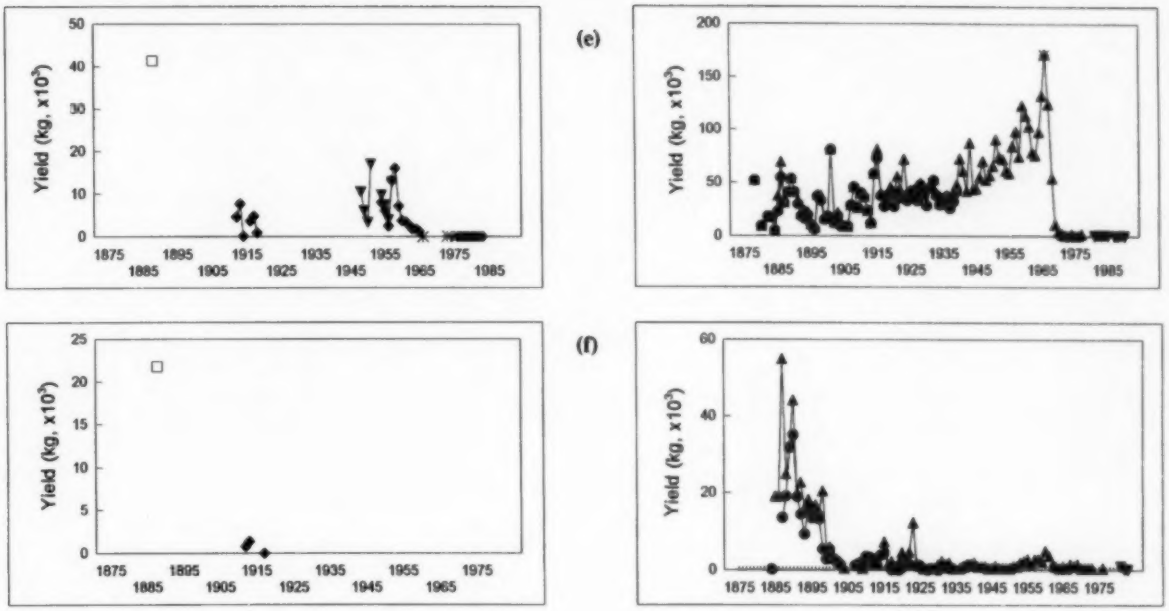
Fig. 6 *(continued).*



The yield of all species harvested from Nipigon Bay, prior to the closing of the commercial fishery in 1984, was ≈8% of the reported maximum in 1910 and ≈30% of the yield that was sustained during the 1940s and 1950s. Yields of whitefish were approximately one third of that sustained during the 1940s and 1950s and lake trout, walleye, and herring yields were <10% of that harvested during the 1940s and 1950s.

Remediation

Probably the first efforts at increasing abundance of target fish species was the removal of fish thought to prey on eggs or young of brook trout. Walleye, northern pike (*Esox lucius*), suckers (white (*Catostomus commersoni*), longnose (*Catostomus catostomus*), and redhorse (*Moxostoma* sp.) species), lake sturgeon, and whitefish were deliberately removed, from the Nipigon River at least, between 1902 and 1921 (Annual Reports, Fisheries Branch, Province of Ontario, Toronto, Ont., summarized by MacCallum (1990)). Records are incomplete but 10 000 fish (70% were northern pike, which are present today but not common (Kelso 1977)) were removed in 6 weeks during summer 1906 (Annual Report, Ontario Department of Fish and Game, Toronto, Ont., 1906). In 1903 and 1912, walleye comprised >40% of the fish removed (Annual Reports, Ontario Department of Fish and Game, Toronto, Ont., 1903, 1912).

Introductions of eggs, fry, fingerlings, and adults of brook trout, lake trout, arctic grayling (*Thymallus arcticus*), and walleye into Nipigon Bay have occurred irregularly since 1914 (Table 1). The first capture of an intentionally introduced species was rainbow trout, introduced into Thunder Bay between 1894 and 1899 (Goodier 1985) and caught soon after in Nipigon Bay (Annual Report of the Fisheries Branch, 1902) and Lake Nipigon (Annual Report of the Fisheries Branch, 1905). Eggs taken from brook trout in the Nipigon River between 1900 and 1920 were returned to the watershed (Ontario Department of Fish and Game Annual Reports 1900–1920) as fry, and the lower river was stocked annually between 1920 and 1957 with progeny from Lake Nipigon and Nipigon River brook trout. Walleye fry and fingerlings (Table 1) were stocked between 1976 and 1985, more than were stocked of any other species. Adult walleye were introduced in 1991–1992, the number (12 134) approximating 30% of the estimated 1957 abundance (Ryder 1968et al). Adult walleye introduced in 1990–1992 came from three genetically distinct stocks (Ihssen. 1992), which allows identification of parents of any recruits.

Attempts to reduce harvest and rehabilitate fisheries included restrictions on harvest by anglers and commercial fishers, regulating and finally eliminating commercial licences, restricting seasons by species (commercial and anglers), and controlling harvest (commercial and anglers). Licensing has been in place since at least 1887 (Arthur 1973). By 1895, five commercial licenses were held in Nipigon (Goodier 1982), but none were allowed as of 1984. In 1919, the daily limit for brook trout was 30 fish or 10 lb (1 lb = 0.454 kg), and the season was closed 15 Sept. to 30 Apr. (MacCallum 1990), whereas now the limit for brook trout is two fish. There has been no fishing season for walleye since 1988.

Because the declines in lake trout populations were attributed to sea lamprey predation (e.g., Lawrie and Rahrer 1972; Smith and Tibbles 1980), a lamprey reduction program began in 1955. An electric lamprey barrier was installed on the Jackfish River 1955–1959 (Sea Lamprey Control Centre) and the first chemical application to the Nipigon River was in 1964. Both the electric barriers and lampricide chemical applications are reputed to have killed walleye, whitefish, and other non-

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target teleosts (summarized by Wilson 1990), but assessments are incomplete.

Treatment of domestic and industrial wastes has improved (RAP 1991, see footnote 3) although effluents from Red Rock, Nipigon, and the Domtar mill continue to produce elevated levels of bacteria and epiphytic algae while locally impaired water quality and macroinvertebrate communities exist (Nipigon Bay RAP Team 1994, see footnote 3). Attempts to rehabilitate substrates included the removal of bark, wood debris, and log- and vessel-handling facilities from the old mill site. Logs have been removed from the lower 5 km of the Nipigon River, and debris has been removed from pools and backwaters.

Stakeholders have recently developed a water management plan for Lake Nipigon and the Nipigon River to maximize water use for the array of water users. Flow rates and water levels will be managed to provide for requirements of spawning fishes, reduced bank and shore erosion, restoration of nearshore macrophytes, and enhanced macroinvertebrate production while maintaining an acceptable level of electricity generation. In conjunction with water level management, upwelling areas have been created to provide trout spawning habitat in the lower Nipigon River. The banks of Clearwater Creek, near Nipigon (Fig. 1), have been recently stabilized, and new waterfront development in Red Rock has included aquatic habitat diversification all in an attempt to restore stable physical features of the landscape.

Linkage between perturbations and remediation of fish community

The changes in the fishery seem only partly linked to events that affected habitat and environment. Periods of greatest change in yield and species composition of the fishery were during the late 1800s to the early 1900s and again in the 1950s and 1960s. Changes to physical habitat were extensive beginning in the late 1800s and continuing until river modification to enhance log drives was complete in the 1960s. Alteration of river discharge and morphometry began in the 1920s and continued until the 1950s. The Red Rock mill began waste discharge in the late 1930s and continues to discharge though with improved waste treatment. Pesticides, including those used for lamprey management, were applied 1950–1970. The greatest admixture of perturbations (physical change, chemical alteration, and fish exploitation) probably occurred in the 1950s and 1960s.

These diverse ecosystem perturbations occured at times when stocks were noticeably declining; however, no single stress appears related to the change in abundance or harvest of any one species. Rather, different combinations of stress existed during different periods of change in the fisheries. Similarly, combinations of actions to reduce stress have resulted in, at least, enhanced recruitment of walleye and brook trout. No evidence of walleye recruitment between 1970 and 1990 exists (Onatrio Ministry of Natural Resources (OMNR) and Department of Fisheries and Oceans (DFO), unpublished data). Since 1991, six walleye progeny between 1 and 3 yr old have been found. In spring 1994, larval walleye were found in the Jackfish (1 larvae per 3500 m^3) and Nipigon (0.2 larvae per 3500 m^3) Rivers. Brook trout are currently depositing eggs in areas where upwellings have been created (R. Swainson, OMNR, personal communication). Uncertainty remains whether enhanced production will result in increased recruitment to the fishery.

That contamination from either insecticide application or mill effluent affected fish reproduction cannot be ruled out. If the former affected reproduction of fishes as it appears to have affected wildfowl (Postupalsky 1970), the 20 yr of reduced (atmospheric) loading after cessation of DDT use in 1970 could contribute both to decreased body burdens of organic contaminants in fishes and should enhance the probability of successful reproduction. Low contaminant levels in fish (German 1968; Kaiser 1977) indicates that DDT and its metabolites and PCB were not likely impairing reproduction. Ryder (1968) implicated the Red Rock mill in the precipitous decline in walleye abundance that occurred in the 1960s and yet the mill was in operation long before the walleye declined. Biochemical reproductive effects from TFM (Munkittrick et al. 1994) and paper mill effluents (Van Der Kraak et al. 1992) and Ryder's (1968) study of Nipigon Bay walleye indicate that chemical contaminants could still be affecting reproduction and early survival.

Species that have exhibited the greatest change (walleye, brook trout, lake sturgeon (Fig. 6), and lake trout) reproduce in streams or are highly dependent upon nearshore Nipigon Bay environments for their well being (Scott and Crossman 1973; MacCallum 1990; Wilson 1990, 1991). Whitefish and lake herring, the least affected among the historic fish community of Nipigon Bay, are less dependent upon tributaries and the nearshore environment (Scott and Crossman 1973; Hansen 1990, 1994). In the 1980s, the average annual harvest of lake whitefish was greater than the period preceding peak sea lamprey abundance (Hansen 1994). Eutrophication, nearshore habitat alteration, and exploitation (reduced because of closure of the commercial fishery and restrictions to angler harvest) also remain as stressors. Developments aiding ecosystem rehabilitation include Nipigon River water level management, habitat improvement by log removal and shoreline restoration, cessation of log drives, and increasing adult walleye abundance. These actions may have resulted in sustainied or new recruitment for walleye and brook trout. Clearly the Nipigon Bay region has historically featured multiple stressors and multiple and complex species responses, but the Nipigon Bay ecosystem is not unique in this respect. Rather the removal of several stresses, reductions in others, and direct intervention have introduced some recent successes. Because multiple stresses are ubiquitous in ecosystems and response to individual stress difficult to identify (Cairns and Niederlehner 1989), it is perhaps logical that restoration should proceed by providing relief to multiple stresses wherever possible producing a response that may not be directly attributable to a particular remediation action but which nevertheless benefits the ecosystem as a whole.

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Benefits from incremental additions to walleye spawning habitat in the Current River, with reference to habitat modification as a walleye management tool in Ontario

W.D. Geiling, J.R.M. Kelso, and E. Iwachewski

Abstract: We increased the area used by walleye (*Stizostedion vitreum vitreum*) for spawning from 143 to 711 m² in the Current River, Lake Superior, to test if *(i)* the abundance of spawning walleye increased in response to greater availability of spawning habitat and *(ii)* walleye spawning occurred on the man-made spawning habitat. The abundance of walleye in the Current River during the spawning period remained between 1100 and 1500 animals, 1991–1993. The area containing live walleye eggs increased by approximately five times, but we have no evidence to indicate that total egg deposition increased. From a survey of walleye habitat enhancement methods used in Ontario, we found that the rated success of habitat enhancement was "moderate" (43% of projects) when combined with introduction of walleye to new waters, "low" (17%) when used to augment a self-sustaining population, and 0 when used to support a population where reproduction was limited or lacking. Most evaluations of benefits from walleye habitat enhancement were subjective or preliminary; however, enhancement of spawning habitat rarely appeared to increase adult walleye abundance. Few circumstances may occur in the short term, where benefits from habitat modification are high and results will be unequivocal

Résumé : Dans la rivière Current, dans le bassin du lac Supérieur, nous avons porté de 143 à 711 m² la superficie pouvant servir de frayère au doré jaune, afin de vérifier (*i*) si l'abondance des géniteurs augmente avec celle des habitats disponibles pour la fraye et (*ii*) si le doré jaune se reproduit dans les frayères artificielles. De 1991 à 1993, le nombre de dorés présents dans la rivière en période de fraye s'est maintenu entre 1100 et 1500. La superficie oj il y avait des oeufs vivants a quintuplé, mais rien n'indique que la quantité totale d'oeufs pondus ait augmenté. Un examen des méthodes utilisées en Ontario pour améliorer l'habitat du doré jaune nous a permis de constater que ces mesures ont eu un succès coté *modéré+ (43 % des projets) lorsqu'elles avaient été combinées à l'introduction de dorés dans un nouveau secteur, *faible+ (17 %) lorsqu'elles avaient pour but d'accroître une population déjà capable de se maintenir et *nul+ lorsqu'elles visaient à soutenir une population dont la reproduction était déjà limitée ou absente. Dans la plupart des cas, l'évaluation des avantages procurés par l'amélioration des frayères était préliminaire ou subjective. Cependant, il était rare que ces mesures augmentent sensiblement l'abondance des adultes. A court terme, peu de circonstances pourraient faire en sorte que la modification des habitats produise des avantages importants et des résultats sans équivoque.
[Traduit par la Rédaction]

Introduction

The Canadian waters of Lake Superior supported four major populations of walleye (*Stizostedion vitreum vitreum*) that perpetuated into this century (Schram et al. 1991). Of these, the Nipigon Bay population collapsed by the early 1960s (Ryder 1968; MacCallum and Selgeby 1987), the Black Bay population collapsed in the late 1960s (Colby and Nepszy 1981), and the Whitefish Bay population collapsed in the 1970s or early 1980s (Schram et al. 1991). In each case, overexploitation was suggested as part of the cause of decline. Efforts through 1988 to restore these populations by stocking (fry, fingerlings, limited adult transfers) have either failed or the results are inconclusive (Schram et al. 1991).

An apparently self-sustaining population of walleye remains in Thunder Bay (Fig. 1A). This population spawns in the Current River and is reported to spawn in the Kaministiquia, Pine, and Pigeon rivers (Schram et al. 1991). The Thunder Bay population also may spawn in the Neebing River, but this river probably ceased producing walleye prior to 1915 as a result of cultural modification of the waterway (A.J. McNab, March 8, 1915, as cited by Goodier 1982).

Schram et al. (1991) suggested that the remnant Thunder Bay walleye population was probably limited by loss of habitat. Construction of docking facilities and dredging of an access channel in 1984 are the most recent in a series of events that have resulted in a loss of walleye spawning habitat in the Current River. In an attempt to offset this loss we augmented remnant, or created new, spawning areas in December 1991. We used this increase in potential spawning area in the Current River to test (*i*) whether the abundance of spawning walleye

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Fig. 1. (A) Location of Thunder Bay within Lake Superior. (B) Lower Current River within the City of Thunder Bay, showing cultural features, remnant spawning habitat, and spawning substrate addition sites.

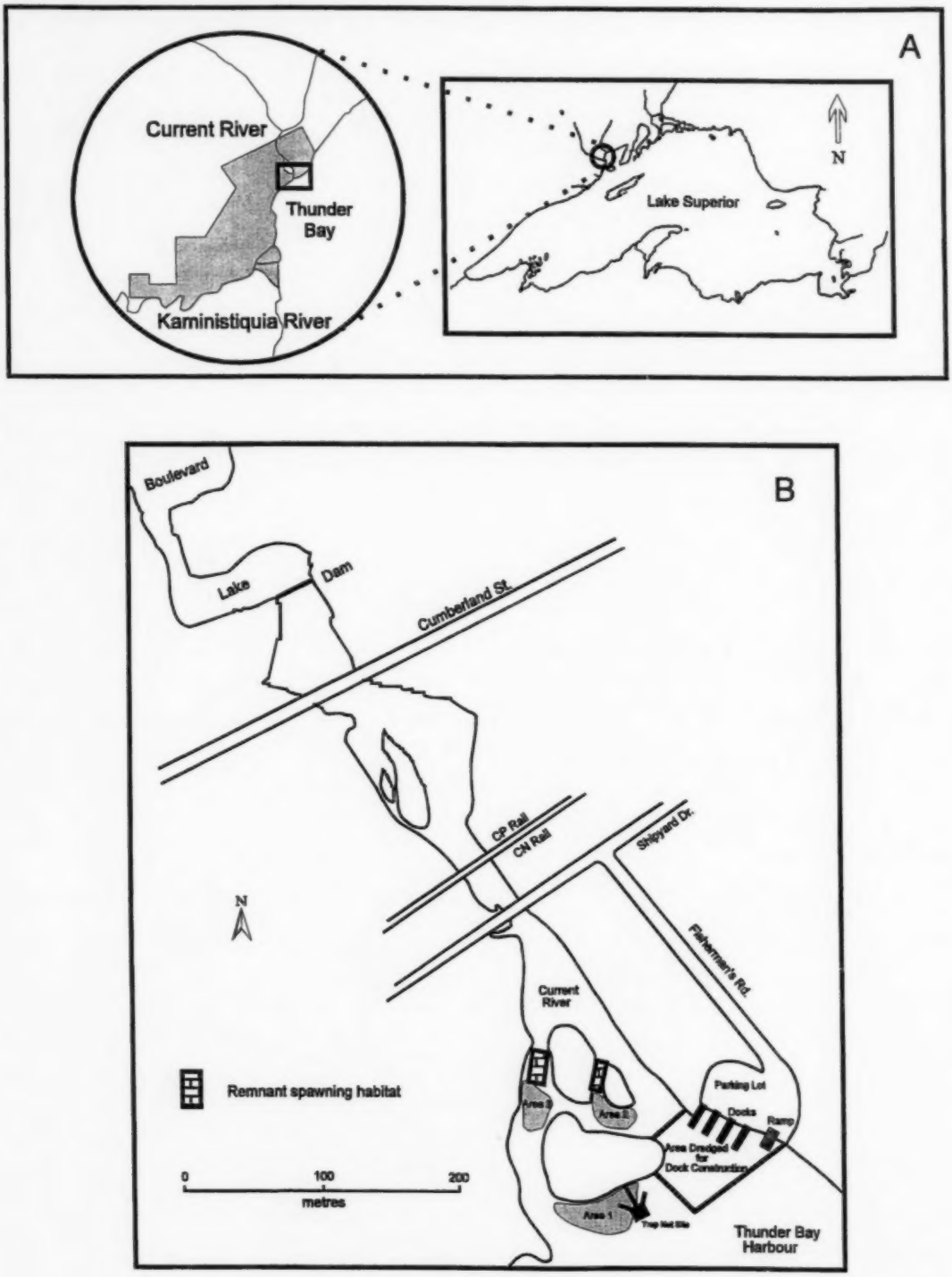

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Table 1. Summary of walleye and walleye egg removals from the Current River.

Year	Month	Walleye removed	Source
1944	May	750 000 eggs	*a*
1970	Aug.	420 adults and juveniles	*b*
1971	July	200 adults and juveniles	*a*
1972	Sept.	616 adults and juveniles	*c*
1984	May	Eggs stripped from up to 15 females	*d*

[a] B. Hamilton, Ontario Ministry of Natural Resources, Thunder Bay, Ont., personal communication.
[b] Black and Sein (1989).
[c] Ball (1988).
[d] E. Iwachewski, unpublished data.

increased in response to greater availability of spawning habitat and (*ii*) whether walleye spawning occurred on the man-made spawning habitat. The Current River example of spawning habitat enhancement is compared with walleye spawning habitat enhancement projects in other Ontario waters.

Historical perspective: Current River estuary and walleye

As early as 1865 a stamping mill at the mouth of the Current River served an upstream silver mine. Both the mill and the mine were closed by the turn of the century. By 1910, a dam was constructed 650 m upstream from the river mouth to supplement electric power supply in what is now the City of Thunder Bay (Fig. 1B). Railway bridges were built across the river in the 1880s, and two road bridges were built over the river in the early 20th century. A sawmill and groundwood pulp mill operated near the mouth of the river in the early 1900s; the sawmill remained in operation until the early 1960s. A fish hatchery, to provide lake whitefish (*Coregonus clupeaformis*) fry to western Lake Superior, was constructed beside the estuary in 1911 and continued in full operation until 1934 (Goodier 1982). The hatchery continued in sporadic operation until the mid-1960s.

In 1984, a boat launch and docking facility were constructed on the north shore of the estuary (Fig. 1B). Construction of docking and boat launching facilities included dredging the docking area and an access channel to Thunder Bay Harbour. The area dredged received the flow of the main river channel, was in waters less than or equal to 2.5 m deep, and had a mixture of gravel, cobble, and boulder overlaying hard-packed silty clay. Dredging removed much of the current-washed rocky layer and changed depths so that the majority of the area near the main channel became deeper than 2.5 m. Potential walleye spawning habitat, defined by waters 0.15–2.4 m deep flowing over a cobble, gravel, and boulder substrate (Hartley and Kelso 1991) was reduced from 3160 to 910 m^2 at the mouth of the main channel. Included in this reduction was virtually all of the potential spawning habitat in the area of main flow.

Goodier (1982) reported an average annual combined harvest of walleye and northern pike from Thunder Bay of 50 000 kg in the peak years 1907–1911. After 1911, harvest declined and commercial landings of walleye from all Canadian waters of Lake Superior ranged from approximately 450 to 1850 kg in the years 1971–1977 (Baldwin et al. 1979). Commercial fishermen are currently restricted to a 25 kg annual incidental catch of walleye for the Thunder Bay area. Between 1980 and 1992, reported landings of walleye in Thunder Bay ranged between 2 and 128 $kg \cdot yr^{-1}$ (G. Forward, Ontario Ministry of Natural Resources, Thunder Bay, Ont., unpublished data). Since 1970, as many walleye have been removed from the Current River estuary (Table 1) for transfer or stocking in other northwestern Ontario locations as have been harvested in the commercial fishery. Angling occurs, but the harvest is unknown.

Methods

Current River spawning habitat enhancement

We chose three areas in the Current River estuary in which to augment existing, or create new, walleye spawning habitat in December 1991 (Fig. 1B). Area 1 (925 m^2), on the south side of the main island at the mouth of the river, is subject to wave action from the lake but is protected from river flow except during floods. Some of the Current River walleye stock may have historically spawned on this small shoal (E. Iwachewski, personal observation). Areas 2 (375 m^2) and 3 (275 m^2) were downstream from existing spawning sites (Fig. 1B) in the middle and secondary channels, respectively. The areas of the existing spawning sites were 82 m^2 in the middle channel and 61 m^2 in the secondary channel.

We did not affect existing spawning habitat. By duplicating upstream channel width, depth, flow diversity, and substrate characteristics where walleye spawned, we hoped to achieve similar characteristics in areas 2 and 3. Area 1 provided a spawning area sheltered from direct river flow. Substrate particle size, materials (Fig. 2), and water depth at existing spawning sites also matched criteria summarized by Hartley and Kelso (1991) and these criteria were used to select the materials and placement at the new spawning sites. All added substrate was clean, local igneous stone. Gravel (5–20 mm diameter) and cobble (100–250 mm) were evenly spread over areas 1, 2, and 3. Boulders (500–750 mm) were randomly placed on the gravel and cobble in areas 2 and 3, and on the cobble in Area 1 prior to gravel placement. Substrate placed in Area 1 followed the existing bottom contour, with water depth ranging from 0 (along shore) to 2.0 m. Mean water depth over the gravel–cobble substrate was 29 cm in Area 2 and 20 cm in Area 3.

Current River walleye assessment

Walleye abundance was estimated in 1991, 1992, and 1993 using the Schumacher multiple mark–recapture method (Ricker 1975). A trap net was installed at Area 1 (Fig. 1B) from the end of April to mid-May and emptied daily. All walleye were removed from the net, measured, and marked with an individually numbered Floy tag. The first two or three dorsal fin spines were removed and kept for ageing.

Catch-per-unit-effort (CUE) data were compared using a one-tailed *t*-test (Lotus Development Corp. 1993). Total length distributions for the pooled 1972 and 1973 samples were compared with the pooled 1992 and 1993 samples using the Kolmogorov–Smirnov test (SYSTAT Inc. 1992). The abundance of walleye that used the Current River estuary for spawning in the early 1970s was approximated by multiplying the mean Schumacher estimate for the years 1991–1993 by the ratio of the 1972 CUE to the mean 1991 to 1993 CUE.

A survey to estimate the distribution of walleye eggs in 1991 using SCUBA indicated that eggs were distributed in patches (<0.25 m^2) of gravel and cobble substrate. We determined the presence of walleye eggs by removing surface cobble and boulders, waving a hand over the substrate, and watching for eggs dislodged from the substrate. Because of the heterogeneity in substrate and egg deposition, we determined the area of substrate containing living eggs and not density. The 1991 assessment of egg distribution by SCUBA was

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Fig. 2. Current River substrate, 1991, near the small island upstream of Area 2. Walleye eggs were found in the cluster of gravel and cobble to the right of the diver's thumb.

Table 2. Abundance estimates (95% confidence intervals in parentheses) and catch-per-unit-effort for walleye caught in a 1.8-m trap net at the mouth of the Current River.

Year	Set date	Removal date	Total catch	Catch per night[a]	Schumacher estimate
1972[b]	Sept. 6	Sept. 15	724	80.4 (68.7)[c]	
1991	April 30	May 16	319	19.9 (19.7)	1167 (938–1544)
1992	April 30	May 14	345	24.6 (16.8)	1188 (923–1668)
1993	April 28	May 13	480	32.0 (22.2)	1485 (1098–2293)

[a]Values are means with SDs given in parentheses.
[b]From Ball (1988).
[c]Standard deviation calculations ignore catch of 124 walleye in a four-night continuous set, Sept. 8–11.

duplicated in 1993. In both years, the SCUBA surveys were timed to occur after the completion of spawning and less than 3 wk from the estimated start of spawning. We began searching for eggs just below a bedrock sill that forms an obstacle for passage of walleye at the upstream end of the secondary channel (Fig. 4). Divers searched from shore to shore working downstream at approximately 2–m intervals.

Walleye habitat alteration survey

To determine the frequency of habitat alteration as a means to enhance or restore walleye populations in Ontario, we surveyed Ontario Ministry of Natural Resources (OMNR) staff. Staff from four Great Lakes Management Units and from 25 land-based units were contacted. We requested information on the rationale for each project, methods, the pre- and post-project assessment strategy, and the success estimated or perceived for the project.

Results

Current River walleye

Trap-net CUE (Table 2) was significantly higher in the fall of 1972 than in the spring of any of 1991–1993 (one-tailed t-test, P range = 0.021–0.031, $\alpha = 0.05$). One net set of four nights duration, September 8–11, 1972 ($n = 124$), was excluded. The higher 1972 CUE occurred after 620 adult and juvenile walleye were removed from the Current River estuary in 1970 and 1971 and transferred to inland lakes.

Walleye captured in 1992 and 1993 were, on average, larger (Kolmogorov–Smirnov test, $P < 0.001$, $\alpha = 0.05$) than walleye captured by similar gear (1.8–m trap net) in 1972 and 1973 (Fig. 3B). The mean length of walleye age-classes also appears to be greater in 1992 than in 1973 (Fig. 3A). We did not test the apparent difference in mean length of walleye age-classes as we only had summary data from 1973, and ageing structures differed between 1973 (scales) and 1992 (dorsal spines). Proportionately, smaller walleye were fewer in the catches in the 1990s. If an inverse relationship between walleye abundance and growth (Colby et al. 1979) exists, the larger sizes of walleye in the early 1990s indicate a decreased population.

Although the total catch (and CUE) of walleye in the Current River estuary increased from 1991 (pre-enhancement) to 1993 (post-enhancement) (Table 2) these differences were not

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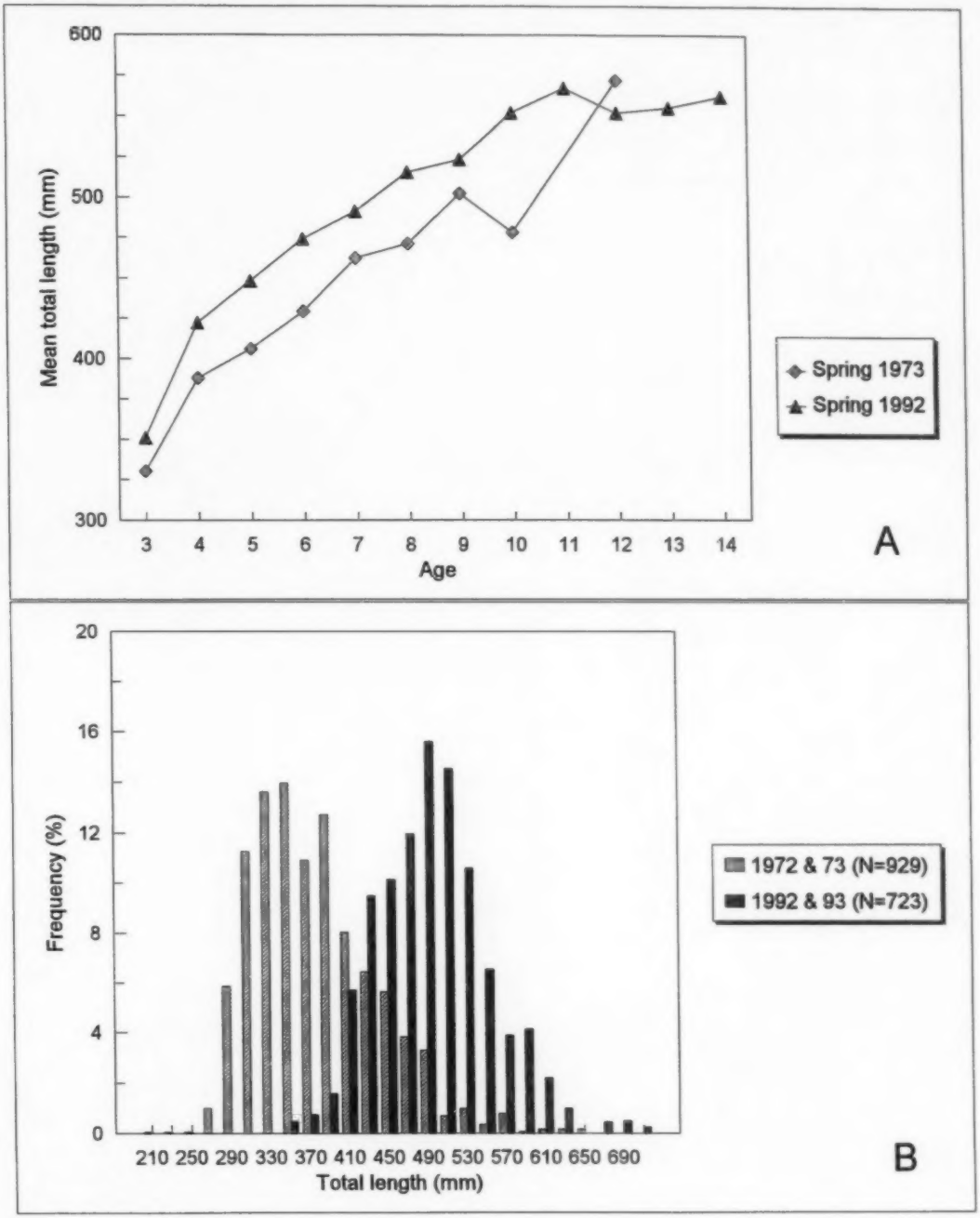
Fig. 3. Mean total length at age (A) and total length distribution (B) for walleye captured by 1.8 trap net in the Current River estuary. Walleye were captured in the fall of 1972 and in the spring of 1973, 1992, and 1993. The 1972 and 1973 data are from Ball (1988).



significant. Using the mean abundance estimate of 1280 and the ratio of the 1972 CUE to the mean 1991 to 1993 CUE (3.16:1) we estimated that 4045 walleye spawned in the Current River in 1972.

In 1972, the Current River spawning population of walleye had available 3303 m² of potential spawning habitat (Table 3). Dredging reduced this amount to 1053 m² in 1984, and only 143 m² was used for spawning in 1991.

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Fig. 4. Areas where living walleye eggs were found in the Current River estuary are labeled with *x* for 1991 and *y* for 1993. The letter *z* is used to mark the area where dead eggs were found in 1991. The area covered by diving surveys is shaded.

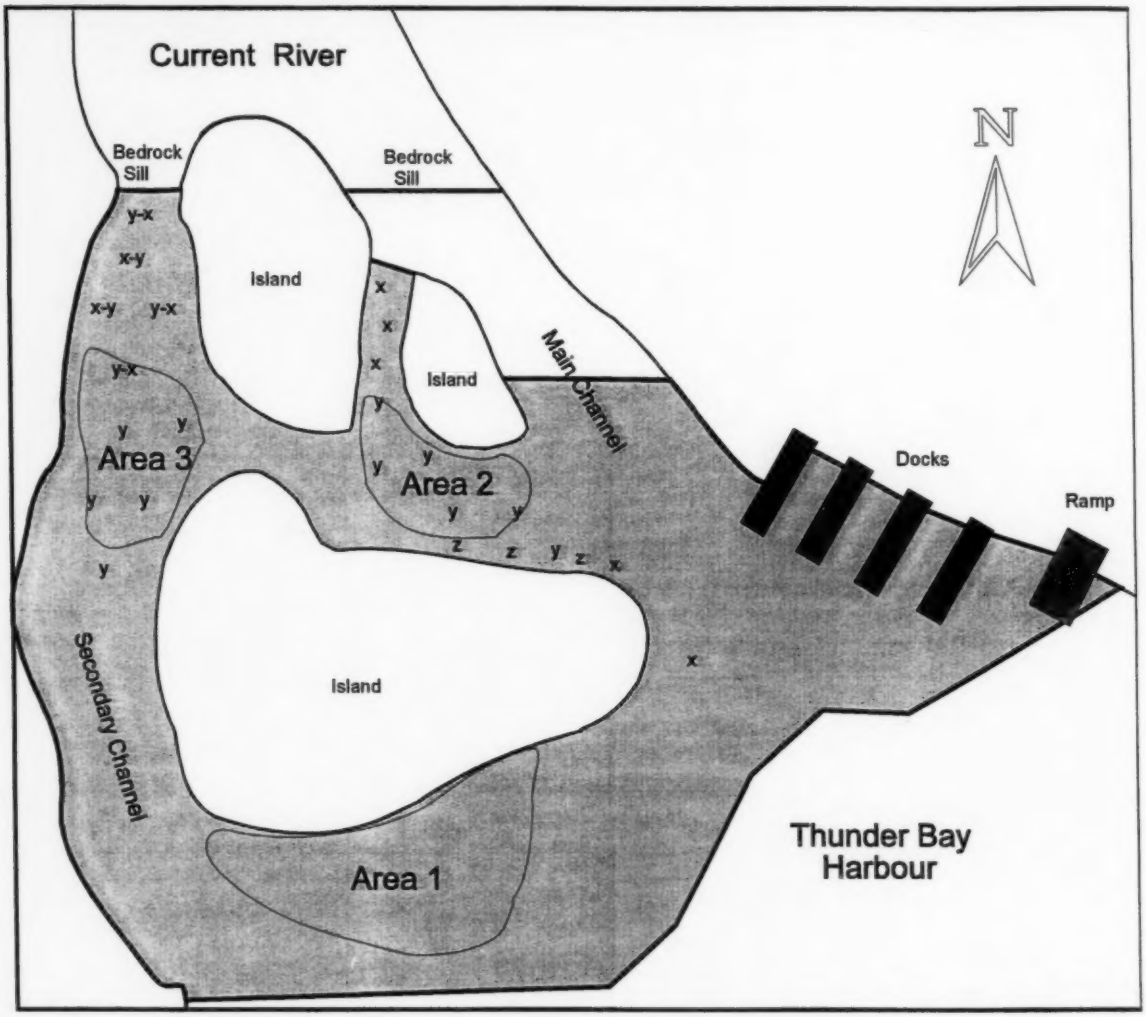

Table 3. Changes in area (m^2) of walleye spawning habitat at the mouth of the Current River.

	Putative historic spawning area (pre-1984)	Putative historic spawning area (post-dredging)	Area used for spawning 1991	Created spawning area	Area used for spawning 1993
Mouth of main channel	3160	910	0	0	0
Secondary channel	61	61	61	275	336
Middle channel	82	82	82	375	375
Lake side of island	na[a]	na	0	975	0
Combined	3303	1053	143	1625	711

[a]na, information regarding use of this area for spawning is not available.

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Table 4. Summary of Ontario Ministry of Natural Resources walleye habitat manipulation project rationales and goals and the total number of times each was cited (No.) by survey respondants.

	Description	No.
Project rationale	In support of an introduction to a location that does not and has not previously supported walleye	4
	In support of a reintroduction to a location from which a walleye population has been extirpated (or very nearly so)	3
	To facilitate reproduction in a location that supports walleye but lacks natural reproduction, or to augment natural reproduction rates that are insufficient to maintain the population	4
	To augment a currently reproducing population	32
	To compensate for habitat lost due to an anthropogenic perturbation	20
	Total	63
Habitat goal	Create or restore access to spawning habitat	7
	Maintain access to spawning habitat	5
	Improve spawning habitat quality	25
	Increase spawning habitat quantity	30
	Decrease deposition of fine sediments	8
	Increase habitat for young-of-the-year	12
	Increase habitat for juveniles and adults	6
	Improve habitat for prey species	1
	Total	94
Biological goal	Increase egg deposition	28
	Increase young-of-the-year production	30
	Increase survivorship of young to adult	14
	Increase adult abundance	21
	Increase growth rate	0
	Create a self-sustaining walleye population	4
	Total	97

In 1991, living walleye eggs were found in substrates just upstream from areas 2 and 3 (Fig. 4) and in the furthest upstream portions of these areas. However, divers reported that siltation was evident around the eggs in the upstream portions of areas 2 and 3 indicating that these eggs may have drifted down from the historic spawning habitats. Few eggs were found in the remnant potential spawning habitat surrounding the dredged zone at the mouth of the main channel, and these may have washed down from the middle channel. A windrow of eggs, the majority of which were dead, was found close to the north shore of the largest island just downstream of Area 2. No living eggs were found in water depths exceeding 2.5 m.

In 1993, walleye eggs were found in the secondary channel in the same habitat as in 1991 and also throughout Area 3 (Fig. 4). Although no quantitative estimates of abundance were derived, divers reported that pockets of eggs, localized by substrate type, were found throughout the area. Eggs were abundant throughout Area 2, but none were found upstream from Area 2 as they had been in 1991. Walleye eggs downstream from Area 2 were apparently fewer in 1993 than in 1991. Eggs were neither found as far downstream in 1993, nor were dead eggs observed along the north shore of the largest island. Overall, eggs were found over 711 m², an approximate fivefold increase from 1991. The substrate added to areas 2 and 3 did not contain fine silt and algae in 1993.

The substrate in Area 1 was covered with epiphytic algae and a fine layer of silt in 1993. No walleye eggs were found by divers in 1991 or 1993.

Walleye habitat alteration survey

Twelve OMNR units reported on 43 projects implemented between 1974 and 1994. Forty of the projects were in riverine or estuarine environments and three were in lakes. Seventeen projects were in tributaries to the Great Lakes – St. Lawrence River. All 43 projects were undertaken, at least in part, to enhance or increase spawning habitat.

Habitat enhancement projects were implemented to augment populations with some reproduction in 32 projects (Table 4). Frequently, walleye habitat enhancement projects had more than one stated goal. Of the 94 habitat goals cited, 55 were to improve the quality, or increase the quantity, of spawning habitat (Table 4). Similarly, 58 of the 97 biological goals were to increase egg deposition or increase young-of-the-year production.

Diverse methods were employed, singly and combined, to enhance walleye habitat. Access to spawning, nursery, and foraging habitat was created or maintained ($n = 14$) by fishway construction, log jam removal, and channel modification including boulder placement. Spawning habitat quantity was increased by the addition of materials adjacent to existing spawning substrate or in areas previously unused by spawning walleye ($n = 30$). Sediment load and deposition in spawning streams was reduced ($n = 5$) by stabilizing stream banks with rip-rap and by augmenting riparian vegetation. Spawning habitat was enhanced by flushing existing substrate and by adding clean rock and rubble to existing spawning areas ($n = 7$). Methods used to increase or improve habitat for young-of-the-year, juveniles, adults, and prey species were the same as those for enhancing spawning success. All projects that increased or improved habitat for young-of-the-year, juveniles, adults, and prey species also targeted spawning enhancement.

Assessment effort was variable, ranging between no assess-

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Table 5. Summary of the degree to which walleye habitat enhancement projects were judged to be successful by survey respondents.

	Project ratings			
	Yes	No	Maybe	Unknown
Were physical habitat targets achieved?	33		5	2
Did project increase the abundance of viable eggs?	13		9	20
Did project increase young-of-the-year abundance?	3	4	13	22
Did project increase adult abundance?	3	6	14	20
Did project maintain the existing adult abundance while supporting increased exploitation?	5	5	9	17
Did project increase growth rates?		24		12

ment ($n = 4$) to quantitative assessment of physical and chemical parameters, egg deposition, larval production, and adult abundance before and after ($n = 3$) the project. However, 33 of 40 projects were judged to have met the desired habitat goals and no projects were judged to have failed (Table 5). Thirteen projects were reported to increase the abundance of living eggs. Only three projects were judged to increase adult populations. Of these three, habitat enhancement supported an introduction or reintroduction of walleye. None of the 29 projects aimed at augmenting reproducing populations were judged to have increased adult walleye abundance. However, five projects (all in the Kenora District) were reported to maintain abundance of spawning adults while supporting increased exploitation.

Assessment of success of the walleye habitat enhancement projects was generally characterized by uncertainty. Responses of "maybe" and "unknown" were more frequent than "yes" and "no" when respondents were asked whether their projects had increased the abundance of any life stage of walleye (Table 5). Some of this uncertainty resulted from the recent (≤4 yr) implementation of 13 projects.

Discussion

Efforts in the Current River sought to compensate for habitat lost by anthropogenic perturbation and, thereby, augment a reproducing population. A simple assumption drove the Current River project and other Ontario projects: reversing losses in habitat that occurred concomittant with a period of population decline should foster the return of walleye populations to the higher abundance previously estimated. However, evidence of the effectiveness of this approach is lacking.

Preliminary assessment from the Current River walleye spawning habitat enhancement project offers limited encouragement. Total catch and mean CUE of adult walleye increased; however, no change in walleye abundance was detectable and the increase in mean CUE from 1991 to 1993 was not significant. Thus, in the short term, the abundance of spawning walleye in the Current River estuary did not increase in response to a fivefold increase in the area of available spawning habitat.

The area of habitat containing walleye eggs in the Current River estuary increased. As the spawning population of walleye remained unchanged and we did not estimate egg density, there is no evidence that the increase in spawning area increased total egg deposition in the estuary. Spawning habitat enhancement simply may have increased the area over which a similar number of eggs were deposited.

It is possible to increase walleye egg deposition and early life survival in lake (Johnson 1961; Newburg 1975), reservoir (Weber and Imler 1974), and riverine (Armstrong and Dyke 1967; Gibson and Hughes 1977; Corbett and Powles 1986) environments by spawning habitat enhancement. None of these studies, however, reported a subsequent increase in adult abundance. McKnight (1975) reported egg deposition rates, excluding zero, were substantially higher on man-made shoals in a small Wisconsin lake than elsewhere in the lake. However, no fry, fingerlings, or adult walleye (<5 yr) were found in the 4 yr following shoal construction despite the reproductive products of resident walleye being proven viable in a hatchery (McKnight 1975).

Laarman (1978) divided walleye stocking programs into three functional groups: introductory, stocking into waters where walleye are absent; maintenance, stocking waters that support walleye but natural reproduction is either limited or does not exist; and; supplemental, stocking to augment naturally reproducing populations. Success was rated as "good" for 48.2% of introductory programs ($n = 27$), 32.5% of maintenance programs ($n = 40$), and 5.2% of supplemental programs ($n = 58$) (Laarman 1978). Rationales for habitat enhancement can be grouped into the same three functional groups. The success for habitat enhancement projects in Ontario (Table 5) would be rated as "good" for 42.9% of introductory projects ($n = 7$), 0.0% of maintenance projects ($n = 4$), and 15.6% of supplemental projects ($n = 32$). Our survey respondents were unable to definitively identify success or failure in the majority of habitat enhancement projects; thus, it is possible that the success rate of the OMNR projects is understated.

The subjective and preliminary nature of habitat enhancement evaluations does not preclude the use of habitat manipulation as a tool for walleye population enhancement. However, the need for long-term, quantitative assessment of habitat enhancement projects is apparent. It is clear that spawning habitat enhancement has become a common, accepted practise without an understanding of when, where, or if it will result in increased adult walleye abundance. Few circumstances may occur, at least in the short term, where benefits are high and results will be unequivocal.

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Habitat models as tools for evaluating historic change in the St. Marys River

K.E. Bray

Abstract: Two habitat models are applied to long-term data to evaluate changes to physical attributes of fish habitat in the St. Marys River in relation to anthropogenic influences related to dredging; infilling; construction of locks, power canals, and dams; and water regulation. The Instream Flow Incremental Methodology for rainbow trout (*Oncorhynchus mykiss*) and the caddisfly (*Hydropsyche* sp.) is used for rapids habitat and the northern pike (*Esox lucius*) Habitat Suitability Index model for areas of aquatic vegetation. These habitats are also examined for long-term change in area. Results indicate that wetland habitat has been lost because of structural changes in localized areas where the physical stresses of shoreline infilling and urbanization have been concentrated. More extensive losses in rapids habitat occurred and increased fluctuations in habitat suitability because of continuing human influence in the rapids are affecting habitat in the river. Habitat change is probably not the sole cause of reported fish community changes. For example, substantial natural change has occurred because of fluctuations in water levels. However, the application of habitat models can provide a useful benchmark tool in retrospective analyses where a long-term data set exists.

Résumé : Nous appliquons deux modèles d'habitat aux données à long terme pour évaleur les changements d'attributs physiques subis par l'habitat du poisson dans la rivière St. Marys par suite des interventions anthropiques dans le domaine du dragage, du colmatage, de la construction d'écluses, de canaux d'amenée et de barrages hydroélectriques et de la régulation des eaux. Nous faisons appel aux méthodes des charges croissantes d'eaux de ruissellement pour la truite arc-en-ciel (*Oncorhynchus mykiss*) et pour la phrygane (*Hydropsyche* sp.) pour ce qui est de l'habitat des rapides, et au modèle de l'indice d'adéquation de l'habitat du grand brochet pour ce qui est des zones de végétation aquatique. Nous nous intéressons aussi à l'évolution à long terme de la superficie de ces habitats. Les résultats montrent que l'habitat des terres humides a diminué en raison des changements structurels survenus dans des zones bien délimitées où les tensions matérielles du colmatage littoral et de l'urbanisation se sont concentrées. Des pertes plus considérables de sont produites dans les rapides, et les fluctuations accrues de l'adéquation de l'habitat dues aux interventions humaines incessantes dans les rapides agissent sur l'habitat de la rivière. Le changement d'habitat n'est probablement pas l'unique cause des changements signalés dans l'ichtyofaune. Par exemple, des changements naturels considérables se sont produits par suite des fluctuations du niveau d'eau. Toutefois, l'utilisation de modèles d'habitat peut donner un point de repère utile dans les analyses rétrospectives quand il existe un ensemble de données à long terme.
[Traduit par la Rédaction]

Introduction

Retrospective analyses of fish communities or environmental conditions affecting fisheries are recognised as important contributions to ecosystem management (Minshall et al. 1985; Steedman and Regier 1987; Petts et al. 1989; Petts 1990). However, most research has focused on community or stock transformations and fluctuations in abundance using information on the physical environment as supporting or corroborating evidence. Few studies have focused directly on habitat or on large river systems, such as the Great Lakes connecting channels. In the past, managers concentrated on the stocks or the harvesters, placing little emphasis on either the role of habitat in fish community structure and stock abundance or the value of managing and protecting habitat per se.

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If rehabilitation represents some return to an earlier functional state (Francis et al. 1979), then knowledge of past conditions is necessary to guide the direction and degree of rehabilitative efforts. The time needed for recovery depends on those variables that require the longest time to adjust. Petts (1987) advises that time scales for recovery or adjustment of ecosystems to stresses imposed by river regulation are often ignored. Petts (1987) suggests that channel substrate and form require the longest period of recovery (close to 100 yr or more) whereas biological communities, such as benthos, vegetation, and fish, adjust in a relatively short time. Therefore, retrospective analyses of structural habitat are particularly important for providing the perspective necessary for rehabilitating systems and functions in the context of long-term ecosystem change.

The quality and quantity of existing information and the technology to retrieve and (or) analyse information are the most significant limitations to retrospective ecological research. Hooke and Kain (1982) suggest the development of indices to allow for quantitative analysis (particularly time series techniques) of data that might otherwise be fragmentary or descriptive. The habitat models used in this study provide a relative measure or index and are useful tools for assessing historical information difficult to compare through time.

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The study area

As the sole outlet of Lake Superior and the largest tributary to Lake Huron, the St. Marys River is an important ecological corridor and provides a variety of habitats for fish and wildlife. The river has also played an important role in the human history of the Great Lakes basin as a strategic waterway, power source, local water supply, and significant food source.

The greatest structural change to the St. Marys River occurred from about 1885 to 1921 (Larson 1981; Osborne and Swainson 1986). Navigation and local industrial interests reshaped the rapids at the head of the St. Marys River through the construction of power canals, locks, and regulatory gates for controlling water levels and flows.

The rich natural resources that attracted people and industry to the St. Marys River area were rapidly exploited. By 1909, commercial fishing in most of the river was halted (Schneider and Leach 1979) and by 1939 was banned in Potagannissing Bay (Michigan Department of Conservation 1961) following complaints of declining catches. Commercial fishing is now allowed in the upper reaches near Gros Cap and the extreme lower end of St. Joseph's Channel (Krishka 1989).

Of the more than 80 species of fish now found in the St. Marys, 12 have been introduced within the last 100 yr, only 5 species intentionally (Emery 1985; Duffy et al. 1987). With the exception of Atlantic salmon (*Salmo salar*), most species introduced into the river are commonly caught in netting surveys (Grimm 1989). No species are known to have been eradicated from the St. Marys River system, although both the lake sturgeon (*Acipenser fulvescens*) and the lake herring (*Coregonus artedii*) have been placed on the list of threatened species in Michigan (Duffy et al. 1987).

Fish harvest records maintained by Canadian and American authorities from the 1870s to the 1910s, indicate that lake whitefish (*Coregonus clupeaformis*) was the most abundant species in the commercial catch. Sturgeon, walleye (*Stizostedion vitreum*), northern pike (*Esox lucius*), lake herring, yellow perch (*Perca flavescens*), bass (probably smallmouth bass *Micropterus dolomeiu*), suckers (*Catastomus* spp.), and occasionally muskellunge (*Esox masquinongy*), carp (*Cyprinus carpio*), and catfish (*Ictalurus* spp.) were recorded by commercial fishermen in the St. Marys River. Notable declines in whitefish, walleye, lake trout (*Salvelinus namaycush*), sturgeon, and muskellunge were observed by the late 1800s. The Michigan State Board of Fish Commissioners charted a decrease in the relative catch of whitefish in the St. Marys River from 1885 to 1893 despite an increase in the number of nets. Few historical or current records of sport fishing harvests exist. Brook trout (*Salvelinus fontinalis*) from the St. Marys Rapids and small creeks and rivers nearby were important for tourism and sport in the 1800s. Intentionally introduced into the St. Marys River ca 1895, the rainbow trout (*Oncorhynchus mykiss*) had become an abundant species in the rapids by the 1920s and, along with lake whitefish, supported much of the sport fishery. Introductions of pink (*Oncorhynchus gorbuscha*) and chinook salmon (*Oncorhynchus tshwatytscha*) in the 1960s, shifted the rapids' fishery to these exotic salmonids, particularly the pink salmon (Wurm 1987; Krishka 1989). The sport fishery in the lower river has remained centred on walleye, northern pike, lake herring, yellow perch, and smallmouth bass (Westerman and Van Oosten 1939; Wurm 1987; Krishka 1989).

Methods and study design

Data were collected in two stages over a 2-yr period. The first stage was a survey of ecological information for the St. Marys River that was used to narrow the focus for the second stage of data collection. The hydrologic and morphologic records for the St. Marys River are extensive, continuous, and span at least 130 yr for the former and 200 yr for the latter. However, comprehensive or long-term biological data sets for the St. Marys River are scarce for the period involved. Split between two countries and several agencies and having had no commercial fishery for a good part of its recorded history, the St. Marys River has a fragmented documentation.

Assessing the reliability of source material is a crucial step in retrospective analyses. Trautman (1981) considered three criteria for assessing statements in the historical record: (*i*) where there is no evident reason for embellishment of the facts; (*ii*) where the statements agree with ecological principles; and (*iii*) where the same statement is made by several authors. In this analysis, two criteria must have been present for qualitative information to be accepted. For quantitative data, where verification may not be available, e.g., water levels or catch statistics, the information was accepted based on Trautman's criteria and on whether the information was generally accepted by the research community.

The analysis of change to habitat was conducted for the St. Marys Rapids and areas of aquatic vegetation. Each habitat type was examined for areal changes over time (quantity), and each is evaluated for changes in suitability (quality) with either the Instream Flow Incremental Methodology (IFIM) (Bovee 1982; Milhous et al. 1990) or the Habitat Suitability Index (HSI) using an indicator species. The models also help identify important variables contributing to change.

St. Marys Rapids

SigmaScan (Jandell Scientific 1988), a digitizing tablet, and 1 : 20 000 maps produced by the U.S. Army Corps of Engineers and its predecessors were used to measure change in size of area of the St. Marys Rapids. Changes in habitat quality or suitability over time were assessed with the IFIM model, which was applied to rapids habitat using the caddisfly *Hydropsyche* sp. and rainbow trout as indicator species. All benthic macroinvertebrate surveys in the St. Marys Rapids (International Lake Superior Board of Control (ILSBC) 1974; Great Lakes Fishery Commission 1979; Koshinsky and Edwards 1981; Duffy, et al. 1987) found high densities of the net-spinning caddisfly genus *Hydropsyche*. Hydropsychids are important food items for rainbow trout, brook trout, and whitefish (Koshinsky and Edwards 1981) and are known to be affected by changes in river discharge (Cellot et al. 1984; Munn and Brusven 1987).

Discharge at the St. Marys Rapids is controlled by 16 gates operated by the U.S. Army Corps of Engineers. The area flooded and estimated mean water depths were obtained from ILSBC (1974) at four standard gate openings: 16, 4, 1, and 0.5. As the discharge at the 16 gate setting was known, it was possible to calculate the remaining three discharge values using the equation derived by the Coordinating Committee on Great Lakes Basic Hydraulic and Hydrologic Data (1970): $Q = a(\mathrm{SWP} - b)^{1.5}$, where Q is the discharge, SWP is the Southwest Pier water level at International Great Lakes Datum 1955, and a and b are equation constants that relate to the number of gates open. As no constants are available for a

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0.5 gate setting, the discharge was estimated using rating curves (Koshinsky and Edwards 1981).

The rapids area was divided into five areas or cells. For each cell at each of the four discharges, the area flooded and mean depth were calculated. A weighted useable area (WUA) for each cell and each indicator organism was then obtained by applying the equation: $WUA = ASI_d$, where A is the area of the cell and SI_d is the suitability index for mean depth of the cell. The WUAs were then summed and transformed into total percent WUA. The relationship between discharge and total percent WUA was derived from a line of best fit for each indicator organism and life stage. For comparison with the WUA estimates for each species, the relationship between total area flooded and discharge (no weighting factors included) was computed.

Time series of percent WUA for each organism and life stage were prepared by generating percent WUA from the line of best fit equations and known monthly or annual mean discharge over the rapids between 1915 and 1984. During this time period the area and structure of the rapids remained relatively constant.

The SI values for substrate and velocity were not included because neither could be satisfactorily estimated. Substrate information for the rapids is not detailed, comprehensive, or quantitative enough to apply to an SI curve. Velocity measurements are also difficult to estimate and could introduce substantial error to the WUA values. An estimate of mean velocity would be of little use in determining species suitability index values. For example, a mean velocity value would most likely result in a SI score of 0 for Hydropsychid organisms that live on or within the substrate. This could create a WUA that would not reflect the actual distribution of the species. As velocity and water depth are dependent variables, it is assumed that using only depth as a weighting factor of area is sufficient to illustrate change. Newcombe (1981) used only depth and velocity to determine instream flow suitabilities for salmonids and suggested that the use of only one variable may be sufficient. Also, although substrate and velocity are considered to be more important in determining habitat suitability for benthic invertebrates, abundance has been found to decrease with increasing depth (Cellot et al. 1984; Jowett and Richardson 1990).

Percent WUA versus discharge was calculated for rainbow trout adult, juvenile, and fry life stages and for the spawning period. All life stages were combined for a total rainbow trout habitat time series using the method described in Raleigh et al. (1984).

Aquatic vegetation

Change in area of submerged and emergent aquatic vegetation along the Canadian shore from Gros Cap to Hay Bay (at Bruce Mines), including St. Joseph Island, was calculated from black and white air photos taken in 1935 (National Air Photo Library, Ottawa), 1949, 1964, 1973, and 1981 (Ontario Ministry of Natural Resources (OMNR)). Complete coverage of the St. Marys River shoreline was available for all years except 1949.

Stands of aquatic vegetation were traced directly from air photos onto acetates and areas were calculated with a digitizing tablet and SigmaScan (Jandell Scientific 1988). Measurements were made in square metres and later converted to hectares. Boundaries for aquatic vegetation were determined from the location of hydrophytic plants, areas within stands of vegetation where open water is visible, the outward limit of emergent or submerged plants, and the upland limit of trees if no other boundary feature could be distinguished.

Existing areas of vegetation were identified with the help of maps, preliminary wetland assessment sheets, and a shoreline videotape (1987). Some areas were verified in 1990 and 1991. Identification of aquatic vegetation on historical photographs was based on vegetation that was seen in the field and related to recent (1981) photographs. Any additional sites were identified based on similarities in photo shade and texture to that of known areas.

The U.S. shoreline was not consistently available on Canadian air photo coverage. Information on current U.S. wetlands and aquatic vegetation and changes through time was obtained from Herdendorf et al. (1981) and Williams and Lyon (1991). Only general comparisons can be made between aquatic vegetation on the U.S. and Canadian shores because Williams and Lyon (1991) used different techniques and identification criteria.

The HSI for northern pike was applied to areas of aquatic vegetation potentially available as fish habitat in the St. Marys River. More important than suitability scores of habitat for the individual year is the comparison among years. The northern pike, an important and abundant game fish in the St. Marys River, is used in the HSI largely because of its strong association with aquatic vegetation and its importance to the river fishery (Liston et al. 1980, 1983: Grimm 1989).

Of the nine variables in the northern pike HSI, five SI scores were estimated from current literature on the St. Marys River, and one was determined from the time series measures of the vegetated area. Total midsummer habitat was calculated by measuring the surface area of river within the 6-m depth contour on U.S. hydrographic charts. According to Liston et al. (1980, 1983), submersed plants are limited to depths less than about 6 m in the St. Marys River. Although northern pike are not limited by depth itself, they avoid the colder and deeper waters and are always found in conjunction with vegetation (Inskip 1982). As temperature profiles for the river were unavailable, the surface area within the 6-m depth contour was used as a surrogate measure of midsummer habitat.

Two variables could not be estimated because of insufficient resolution on the air photos: (*i*) the ratio of spawning habitat to summer habitat, because it requires knowledge of the extent and composition of vegetated bottom cover, and (*ii*) the percent of pools and sluggish water to total area. The measure of total dissolved solids (TDS) is not included as it is not considered to be limiting in riverine systems that have a TDS of <800 ppm (Inskip 1982). In the St. Marys River, TDS is usually <100 ppm (Liston et al. 1980, 1983), and there is no indication that TDS has changed.

Results and discussion

St. Marys Rapids

The St. Marys Rapids area originally consisted of the main rapids and a smaller rapids known as the Belle Isle Cascades between St. Marys Island and the mainland on the north side. Between 1887 and 1915, a 50% reduction (Fig. 1) in the area

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Fig. 1. Areal extent of the St. Marys Rapids and Belle Isle Cascades from pristine to present day conditions, 1885–1985.

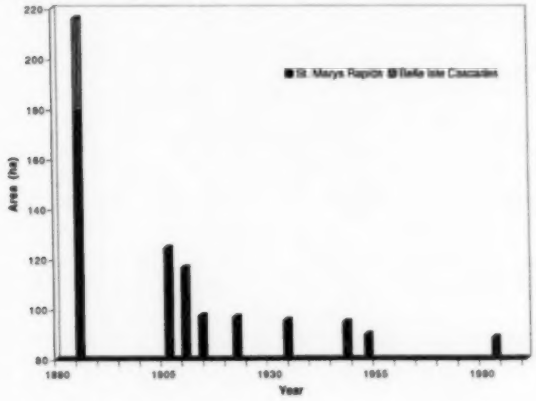
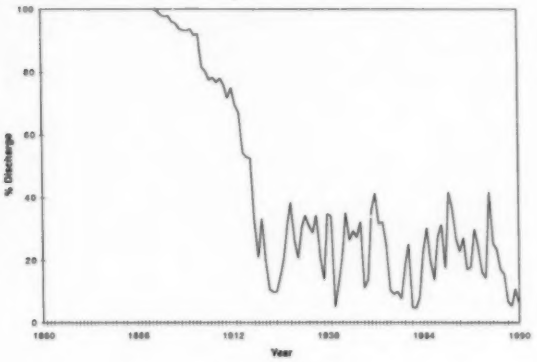


Fig. 2. Mean annual discharge ($m^3 \cdot s^{-1}$) over the St. Marys Rapids as a percentage of the total mean annual discharge of Lake Superior, 1860–1990.



of the main St. Marys Rapids occurred as a result of endeavours to improve navigation and to generate hydroelectric power. Complete elimination of the Belle Isle Cascades, an area considered to have supported a substantial fishery for native peoples (Hunter and Associates 1979), occurred by the 1890s with the development of the site for a shipping lock and industry. If the Belle Isle Cascades are considered when calculating percent change over time in the St. Marys Rapids, the area of rapids lost is almost 60%. The main rapids area (now downstream of the regulatory gates) was isolated from the shoals upstream. Although these shoals still exist, they were dredged for navigation purposes (U.S. Army Corps of Engineers 1886; Canada Department of Public Works, no date) and possibly altered at the time of construction of the locks and compensating works.

Water regulation began in 1921 with the completion of the compensating works. The mean annual discharge over the rapids dropped dramatically and both the frequency and amplitude of low and high discharges increased (Fig. 2). Once the sole conduit of Lake Superior' s outflow, the rapids now typically convey less than 50% of the total discharge and sometimes less than 10%. Most of the flow is directed through power canals and a small percentage through ship locks. Since the potential for hydroelectric power generation was realised in the rapids, there has been argument and negotiation over the distribution of the St. Marys River discharge among power companies. The frequency of high and low flows over the rapids was a concern for both power companies and agencies responsible for maintaining the fishery. The decline of the river fishery was considered by many anglers and some resource managers to have been the result of discharge regulation (Michigan Department of Conservation 1937, 1943).

Fig. 3. Mean annual percent useable area (UA) in the St. Marys Rapids, 1915–1984.

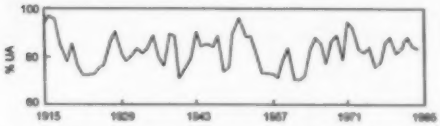
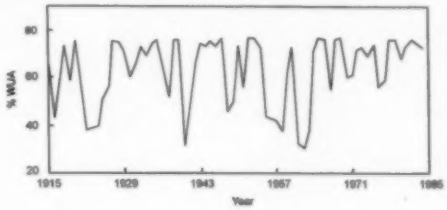


Fig. 4. Mean annual percent weighted useable area (WUA) in the St. Marys Rapids for *Hydropsyche* sp., 1915–1984.



The instream flow analysis

For comparison with the WUA for the indicator organisms, an estimate of only useable area (UA) over time was prepared (Fig. 3). This change in wetted area of the rapids with discharge does not include any suitability factors. Most of the time, more than 70% of the rapids area was under water and potentially available as aquatic habitat with the greatest UA occurring from August to October, the months of highest discharge. All estimates of UA for the indicator organisms are most likely overestimates because only one weighting factor was used.

The relationship between percent WUA and mean annual discharge (Q) (cubic metres per second) for Hydropsychids was found to be described by the equation: $\%WUA = 19.097 + 0.146Q - 0.000\ 092\ Q^2$ ($r = 0.99$; Fig. 4). The r values for all equations in the IFIM are significant at $p < 0.05$.

The assumption that Hydropsychids occupy the entire rapids area may have positively biased the WUA estimate. The most comprehensive survey of benthic macroinvertebrates in the rapids did not include most of the American side, which is generally deeper with a substrate composed of more flat slabs and bedrock, or Whitefish Channel, which was not always flooded (ILSBC 1974). That study concentrated on the south side of Whitefish Island and extended to the international border only at the eastern edge of the rapids. The greatest densities of *Hydropsyche* sp. were found south of the western tip of Whitefish Island above the water's edge at a 0.5 gate setting (Koshinsky and Edwards 1981). The benthic community on

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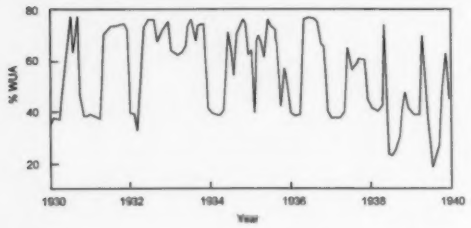
Fig. 5. Mean monthly percent WUA, 1915–1984, for *Hydropsyche* sp. in the St. Marys Rapids.



the American side of the St. Marys Rapids is largely undocumented.

Depth as a suitability weighting factor for Hydropsychids resulted in a %WUA of about 40–80%. A 1 or 0.5 gate setting results in the loss of most of the habitat along the south side of Whitefish Island. Hydropsychids are more likely to be found along riverbanks and in shallow water. This increases the variability in substrate and the availability of food although Hydropsychids have been found in the deeper midchannel areas of large rivers (Cellot et al. 1984). It is conceivable, therefore, that the entire rapids once supported Hydropsychids. In the 1870s, Smith (1874, p. 708) found "great numbers of larvae and pupae and subimagos of *Hydropsyche*" along with molluscs, Diptera, Ephemeroptera, and Chironomids in the stomachs of whitefish taken from the St. Marys Rapids.

Since the loss of most of the American side of the rapids with its channels and islands, the Canadian Whitefish Island area is probably the most productive part of the rapids. Any reduction in discharge that reduced wetted area around Whitefish Island was probably not compensated for by an increase in suitability along the U.S. side. Not only is habitat dewatering a significant negative influence on abundance of net-spinning caddisflies, but the reduction in water velocity in the open channel may also lead to declines in abundance (Weisberg et al. 1990).

From 1915 to 1984, an average of 60–70% of the mean monthly percent WUA was suitable for Hydropsychids. Higher WUA values correspond to the critical periods of caddisfly oviposition, incubation, and hatching. Hydropsychids deposit egg masses in May to September and are believed to have an incubation and hatching period of 8–11 days (Merritt and Cummins 1984). Emergence usually occurs from May until October (Cellot et al. 1984). In a 10-yr mean monthly cycle, however, values as low as 20% WUA can occur in periods of low water (Fig.5). Should velocity and perhaps substrate be added to the equation, the overall percent WUA could drop even lower.

Fluctuations in the abundance of Hydropsychids may be more significant than direct effects of discharge on fish (Irvine et al. 1987). Fish in the St. Marys Rapids may not be limited by space, especially if nearby habitats are not fully exploited or the rapids is used only as a feeding ground. Lake whitefish are found in the rapids almost all year and congregate during their fall spawning season. However, it is unclear whether they actually spawn in the rapids (Koshinsky and Edwards 1981), whereas other areas of the river are known spawning areas for lake whitefish (Goodyear et al. 1982; Behmer et al., no date).

Table 1. Relationship between percent weighted useable area (WUA) and discharge (Q) for IFIM analysis for rainbow trout adult, juvenile, fry, and combined life stages and for the spawning period.

Life stage	Equation of the line of best fit	r
Adult and juvenile	$\%WUA = -106.026 + 28.27 \ln Q$	0.99
Spawning	$\%WUA = 8.833Q^{0.334}$	0.98
Fry	$\%WUA = 69.25e^{(-0.0024Q)}$	0.97
Combined	$\%WUA = -6.74 + 0.211Q - 0.000093Q^2$	0.97

Note: All r values are significant at $p < 0.05$.

The habitat time series for individual and combined life stages of rainbow trout shows much more variation in percent WUA than for the Hydropsychids (Table 1, Fig. 6). The WUA for adult rainbow trout ranged from 20 to almost 100% and for spawning stage rainbow trout, from 40 to 100%. The habitat time series for rainbow trout fry, however, is the reverse image of the adult. The use of mean depth measured across the width of the rapids has negatively biased the fry suitability score. Fry prefer shallower, more sheltered areas (Raleigh et al. 1984; Waite and Barnhart 1992), which in the St. Marys Rapids would include the slower current and increased cover afforded by Whitefish Island and Channel. In years of low discharge, the percent WUA for fry increased while that for the other life stages decreased. Adult and spawning stage rainbow trout %WUA were similarly affected by discharge, the adult stage more negatively affected by lower discharges. The combined life-stage percent WUA estimate (Fig. 7) shows a range of values from a low of near 10% of the total area to fully 100%.

Suitability curves are usually prepared for species in stream habitats as few instream flow studies are done on large rivers. Preparation of site-specific curves is the most accurate way of determining WUA estimates, the lack of which is a criticism of many studies. Waite and Barnhart (1992) used four different curves, including those of Raleigh et al. (1984) that are used in this study, for comparing WUA of rainbow trout juveniles and fry. Waite and Barnhart (1992) found that velocity was the main source of differences in WUA although they also cite another study in which SI curves for depth were the main cause of variation in estimates of WUA. However, all curves in the Waite and Barnhart (1992) study resulted in the same line configuration of WUA, only the magnitude along the y axis was different. The Raleigh et al. (1984) curves were intermediate between those developed by Bovee (cited in Waite and Barnhart 1992) and curves developed on site.

Although the exact dates of rainbow trout spawning in the St. Marys Rapids area are unknown, it is believed that most spawn in June with a possible fall spawning run as well (A. Dupont, OMNR, Sault Ste. Marie District, persopnal communication). Throughout the annual cycle, percent WUA generally increases for adult rainbow trout, but decreases for fry. The increase in discharge in the late summer and fall months results in a lower SI score for fry as a result of increased water depths. If velocity was included as a weighting variable, the WUA estimate for fry could be even lower in the summer and fall months because of the higher discharge.

More than the occurrence of low flows, increased fluctuations in mean monthly and annual discharges over the rapids as a result of flow regulation may be responsible for creating a habitat of increasingly variable suitability. Many researchers

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Fig. 6. Mean annual percent WUA for rainbow trout (A) adult and juvenile, (B) spawning, and (C) fry stages in the St. Marys Rapids, 1915–1984.

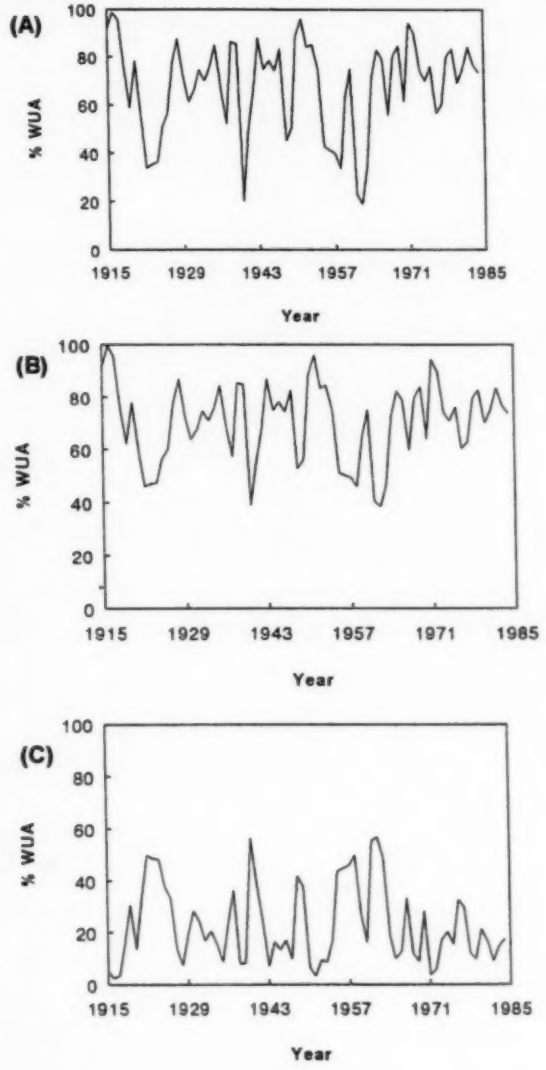
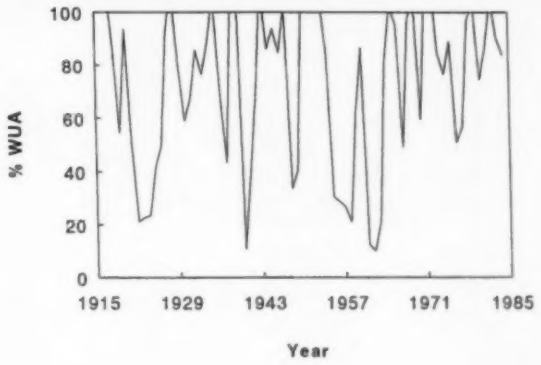


Fig. 7. Mean annual percent WUA for combined life stages of rainbow trout in the St. Marys Rapids, 1915–1984.



have investigated the effects of river and stream flow fluctuations on aquatic organisms (e.g., Peters 1982; Cushman 1985; Nelson 1986; Burt and Mundie 1986; Curry et al 1994). Nelson (1986), for example, found that large daily flow fluctuations generally led to poor yearling crops of brown trout (*Salmo trutta*). He concluded that stream discharge was the most important factor in determining standing crops of trout because of the wide seasonal and annual variations in flow due to stream regulation. Despite the lack of historical daily discharge records for the St. Marys River, the mean monthly and annual flow records indicate the discharge can fluctuate widely. However, habitat for species such as the rainbow trout may not be limited directly by changes in flow of the St. Marys Rapids. Food, spawning substrate, cover, temperature, or competition for space may also play important roles in the distribution and abundance of species in the rapids (Binns and Eiserman 1979; Bowlby and Roff 1986; Irvine et al. 1987).

Aquatic vegetation

Although the areal extent of emergent and submerged aquatic vegetation has fluctuated from year to year, largely in response to changing water levels (Fig. 8, Table 2), there was little decrease of area from 1935 to 1981 as a result of human activities. The total area of aquatic vegetation along the Canadian shore changed with fluctuations in mean annual water level, ranging from 1111 (1981) to 2418 ha (1964). Mean annual water levels ranged from 176.16 to 177.17 m.

Williams and Lyon (1991) found an inverse relationship between water levels and extent of emergent vegetation along the U.S. shore of the St. Marys River. A similar relationship between increasing water levels and decreasing of aquatic vegetation is seen in Fig. 8 for the Canadian shore. The greatest response to changing water levels was the change in the extent of emergent vegetation; there was little change in total wetland area over time (1939–1985) (Williams and Lyon 1991).

Most Great Lakes wetlands are maintained in a state of early vegetational succession by interannual changes in water level or "pulse stability" (Herdendorf and Raphael 1986; Williams and Lyons 1991). Exposure to short- and long-term water level fluctuations imposed by the action of the Great Lakes prohibits advanced stages of succession and the eventual transformation of wetland to terrestrial environment (Herdendorf and Raphael 1986).

Williams and Lyon (1991) found that the negative relationship between areas of emergent vegetation and water levels on the St. Marys, while significant, was weaker than for coastal wetlands on Lakes Michigan, Huron, and Erie. They suggest that the wetlands, or areas of emergent vegetation, may exhibit advanced successional growth because of greater protection from wind and wave action. Duffy et al. (1987) claim that, within the past three decades, the plant communities of the St. Marys River wetlands remained relatively stable in composition and distribution, the dominant species being hardy and long lived.

It is unfortunate that no photographic record exists of the

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Fig. 8. Area of emergent and submerged aquatic vegetation (ha) along the Canadian shoreline at mean annual water levels (m) for years measured.

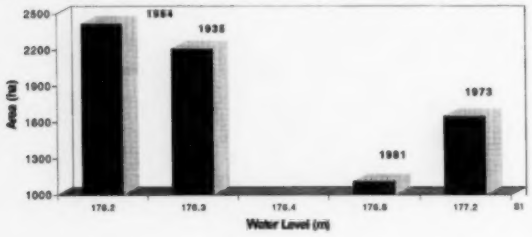


Fig. 9. Mean annual water levels below Sault Ste. Marie, Ont., 1908–1988. Markers indicate years of air photo coverage. Middle line indicates mean annual water level for period.

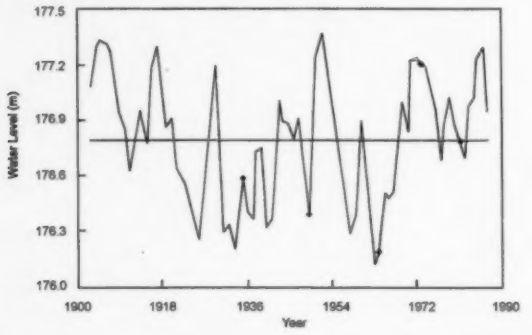
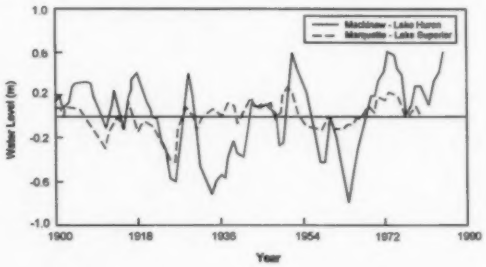


Table 2. Area (ha) of emergent and submerged vegetation along the Canadian shore of the St. Marys River for each year measured and mean annual water level.

	Year and water level (m)				
River section	1981 (176.77)	1973 (177.17)	1964 (176.16)	1949 (176.38)	1935 (176.34)
Upper river to Lake George	548	516	666	Inc	827
St. Joseph Channel	94	217	339	Inc	297
St. Joseph Island	469	918	1413	Inc	1088
Total Canadian shore	1111	1651	2418	Inc	2212

Note: The 1949 air photo series is incomplete (inc).

Fig. 10. Variation (m) in mean annual water levels from the mean on record for Mackinaw City, Mich. (Lake Huron), and Marquette, Mich. (Lake Superior), 1900–1985.



St. Marys River shoreline prior to discharge regulation in 1921 for comparison with postregulation photos. Of the 5 yr of aerial photography analysed for aquatic vegetation, the annual mean water level for 1935, 1949, and 1964 was well below the mean for the period on record, only 1973 was significantly higher, and 1981 close to the mean level (Fig. 9). The greatest change in water level occurred between 1964 and 1973 (1.01 m in 9 yr). However, this change did not correspond to the greatest difference in area of aquatic vegetation. Examination of the annual mean water levels indicates that the area of aquatic vegetation in 1981 should have been higher than in 1973 because the water level had decreased. Between these years, only one year fell below the mean annual water level for the period of record. Continuous high water can cause significant dieback of emergents within 3–5 yr of flooding (Keddy and Reznicek 1986). Emergent vegetation along the shore of the St. Marys River had little opportunity to reestablish, a circumstance that probably continued into the mid-1980s.

With the exception of the 1950s, the years following discharge regulation were mostly low water years until the 1970s. During this time, the large stands of emergent vegetation had the opportunity to become more firmly established in the river. Periodic high water levels would have served to maintain diversity in aquatic plant communities along the water's edge and to cause flooded portions of woody plant and *Typha* sp. communities to die back.

There can be only speculation regarding the areal extent, species composition, and reaction to water levels of aquatic vegetation prior to discharge regulation. Travellers to the area wrote little of the lower river, but a few accounts describe areas of extensive vegetation around St. Joseph Island and smaller pockets along the north shore of St. Joseph Channel (Jameson 1838; Bayliss and Bayliss 1938).

Although the record of water levels for the St. Marys River below the rapids does not extend prior to 1903, the pattern of fluctuations can be compared with a station in Lake Huron, such as Mackinaw City, Mich., which has a long record of water level observations (Fig. 10). Prior to the 1920s, water levels were generally higher, a trend that began in the early 1800s according to Bishop (1990). Periods of lower than normal water levels help establish plant species in deeper areas of the waterbody (Keddy and Reznicek 1986). These events may have been necessary to allow for the expansion of emergent stands, such as occurred in the mid-20th century. It is likely that there is presently more aquatic vegetation because of the four decades of mostly low water that promoted expansion of emergent plant communities.

Fluctuating water levels, however, are not the sole forces acting on aquatic vegetation stands in the St. Marys River. The scouring and eroding action of ice and ship traffic on the outward edge of plant communities is also important, although not well understood (Poe and Edsall 1982; Williams and Lyon 1991). Vessel traffic during ice cover creates more erosion of vegetation than when no ice is present (Poe and Edsall 1982). Effects of ship passage on vegetation stands depend on the site characteristics and not necessarily ship size and speed, although McNabb et al. (1986) found that ship passage generally enriches wetlands through the influx of river sediments.

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Table 3. Northern pike Habitat Suitability Index scores calculated for years of air photo coverage (1935, 1949, 1964, 1973, 1981).

Variable	Year	Value	SI score
Drop in water level during embryo and fry stages (m) (V_2)	1981	Increase	1.0
	1973	Increase	1.0
	1964	Increase	1.0
	1949	Increase	1.0
	1935	Increase	1.0
Percent of midsummer area with emergent and (or) submerged aquatic vegetation (V_3)	1981	≤5	0.3
	1973	≤8	0.4
	1964	≤10	0.5
	1949	Incomplete	Incomplete
	1935	≤8	0.4
Least suitable pH in spawning habitat during embryo and fry stages (V_5) (Edwards et al. 1989)	1981	6.7–8.4	1.0
	1973	6.7–8.4	1.0
	1964	6.7–8.4	1.0
	1949	6.7–8.4	1.0
	1935	6.7–8.4	1.0
Average length of frost-free season (days) (V_6) (Duffy et al. 1987)	1981	110	0.95
	1973	110	0.95
	1964	110	0.95
	1949	110	0.95
	1935	110	0.95
Maximal weekly average summer temperature (°C) (1–2 m deep) (V_7) (Liston et al. 1983)	1981	21–24	1.0
	1973	21–24	1.0
	1964	21–24	1.0
	1949	21–24	1.0
	1935	21–24	1.0
Stream gradient (m/km) (V_9)	1981	0.05	1.0
	1973	0.05	1.0
	1964	0.05	1.0
	1949	0.05	1.0
	1935	0.05	1.0

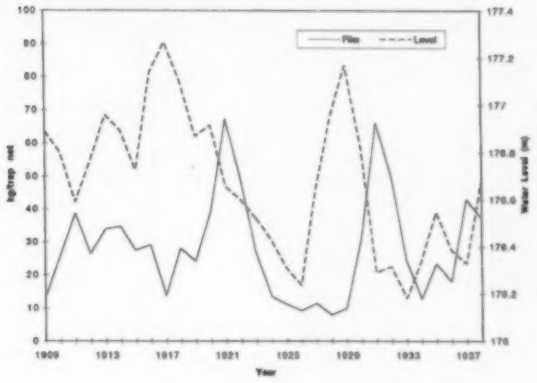
Note: The 1949 air photo series and the water levels are incomplete.

However, McNabb et al. (1986) did not address frequency of passages in their investigation of the hydrologic effects of ship passage on wetlands of Lake Nicolet.

It would appear from descriptions of early travellers to the St. Marys River area and the few air photos taken in the 1920s of the Sault Ste. Marie area that the only real losses of aquatic vegetation occurred prior to regular air photo coverage and were confined to the Canadian shoreline at Sault Ste. Marie and perhaps at Bruce Mines, both urban centres. Early accounts of the area describe the shore at Sault Ste Marie to have been low, wet, marshy ground (Ross 1922).

Low altitude, oblique aerial photography from 1927 and 1928 shows remnants of marshy ground where infilling and construction had not yet occurred. Today, the city' s waterfront has changed considerably and no longer supports aquatic

Fig. 11. Annual catch of northern pike per trap net from Potagannissing Bay, 1909–1938, and corresponding mean annual water levels (m).



vegetation. The aquatic vegetation along the Sault Ste. Marie shoreline may have been important to productivity of the St. Marys Rapids area by providing refuge, nursery habitat, and food production for fish that had no other local wetlands options.

Habitat suitability analysis

The ratio of the area of aquatic vegetation measured from the air photos to the total midsummer area of aquatic vegetation calculated from hydrographic charts was highest in 1964 and lowest in 1981 (Table 3). The total HSI score for northern pike is equal to the lowest suitability score of the variables in the model. The actual score should probably be reversed so that the year of highest suitability would correspond to the year of lowest measured aquatic vegetation. This is not necessarily a fault of the model but rather a result of measuring vegetation from aerial photographs that revealed more vegetation in years of low water levels.

Comparison of the annual catch per trap net of northern pike from one commercial fisherman in Potagannissing Bay from 1909 to 1938 with the corresponding mean annual water levels (Fig. 11) showed higher catches of northern pike occurred 2–3 yr following high water levels. The catches are considered to reflect the relative abundance of fish species in the bay at that time (Westerman and Van Oosten 1939). Risotto and Turner (1985) state that the most appropriate lag time in the investigation of the effects of water levels on fishery yields depends on the time required for the fish to reach size at capture. In the St. Marys River, most northern pike caught in a 1987 fisheries survey in Potagannissing Bay were 1–4 yr old (Grimm 1989). The relationship between greater yields and high water levels appears to result from an increase in area made available not only for spawning, nursery, and shelter, but for food production as well. Inundation of floodplain areas releases valuable nutrients from soils and vegetation (Risotto and Turner 1985; Miranda et al. 1984). Northern pike spawn in areas of flooded emergent and submersed vegetation (Holland and Huston 1984) and benefit from the increased habitat available in years of high water levels.

Results from the empirical measurements and habitat models for indicator species used to investigate changes to the St.

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Marys Rapids and Sault Ste. Marie area are evidence that habitat losses have been mostly restricted to localized areas where urban and industrial development has occurred. However, changes associated with these losses of habitat affect the remainder of the river, particularly through alteration of the hydrologic regime through discharge regulation.

The loss of 50% or more of the St. Marys Rapids area represents a drastic change in habitat and undoubtedly had a major effect on the aquatic community of the rapids and the river. The IFIM model, although applied to the period following most structural change to the rapids, indicates that the remaining habitats may be subject to fluctuations in discharge that affect their size and relative suitability.

Both the empirical measurements of aquatic vegetation and the application of the HSI model indicate that area of emergent and submerged vegetation in the lower river changes mostly with water level. Here too, the only absolute loss of habitat has been in the Sault Ste. Marie area as a result of urban expansion. Although the relative importance of this area of aquatic vegetation for biotic communities is unknown, it may have been significant both as local habitat and as a corridor linking the rapids with the rest of the river.

The results also indicate that, while important, loss of fish habitat or declines in suitability cannot be held solely responsible for the reported declines in fish abundances. Had the losses or modifications of habitat been responsible for the decrease in fish populations, reports of poor fishing should not have occurred until the late 1800s to early 1900s. As it was, complaints of reduced fishing success were documented prior to any substantial structural alteration of the river (Milner 1874).

Rehabilitation has been linked with a return to, or achievement of, a "desired state," which implies the need for human intervention and a knowledge of past conditions. Describing and systematically evaluating previous conditions is often difficult because of inconsistencies inherent in the historical record. Relative measures or indices provided by habitat models, such as the HSIs and the IFIM, can be useful for charting physical habitat change through time, especially where long-term data sets exist.

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Effects of habitat change in the St. Marys River and northern Lake Huron on sea lamprey (*Petromyzon marinus*) populations

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Abstract: The abundance of parasitic and spawning-phase sea lamprey (*Petromyzon marinus*) in northern Lake Huron increased by more than fourfold from 1978 to 1985, remaining high through 1993. We determined whether (*i*) instream rehabilitation in the St. Marys River, (*ii*) improvements in larval habitat quality in the St. Marys River, or (*iii*) increased forage fish biomass and salmonid stocking in northern Lake Huron could account for this population increase. We found no significant changes in larval sea lamprey abundance in the St. Marys River from 1971 to 1992. Furthermore, habitat rehabilitation in the St. Marys River occurred 3-5 yr following the increases in adult sea lamprey. Therefore, improvements in spawning and larval habitat quality and quantity could not explain the increase in parasitic-phase sea lamprey. However, bloater chub (*Coregonus hoyi*), one of the initial targets for recently transformed sea lamprey, increased in biomass between 1978 and 1982. We observed significant, positive correlations between parasitic-phase sea lamprey abundance and bloater chub biomass and lake trout (*Salvelinus namaycush*) and chinook salmon (*Oncorhynchus tshawytscha*) stocking rates. We conclude that the increase in parasitic-phase sea lamprey can be attributed to improved survival of recently transformed sea lamprey resulting from greater prey availability.

Résumé : Entre 1978 et 1985, l'abondance de la grande lamproie marine en phase parasitaire et en phase de reproduction s'est multipliée par plus de quatre, et est demeurée élevée jusqu'en 1993. Nous avons déterminé si cet accroissement de la population pouvaitêtre imputable : (*i*) aux travaux d'assainissement de la rivière St. Marys; (*ii*) à l'amélioration de la qualité de l'habitat des larves dans la St. Marys; ou (*iii*) à l'accroissement de la biomasse de poisson fourrage et à l'ensemencement de salmonidés dans le nord du lac Huron. Nous n'avons pas observé de changements significatifs dans l'abondance des larves de lamproie dans la St. Marys entre 1971 et 1992. En outre, la restauration de l'habitat de la rivière s'est effectué 3 à 5 ans après la hausse de l'abondance des lamproies adultes. Les améliorations qualitatives et quantitatives de l'habitat de reproduction et de celui du stade larvaire ne parvenaient donc pas à expliquer l'accroissement du nombre de lamproies en phase parasitaire. Toutefois, la biomasse de cisco de fumage (*Coregonus hoyi*), une des cibles initiales de la lamproie qui vient de subir sa métamorphose, a augmenté entre 1978 et 1982. Nous avons observé des corrélations positives significatives entre l'abondance de la lamproie en phase parasitaire et la biomasse du cisco de fumage d'une part, et le taux d'ensemencement en touladi et en quinnat d'autre part. Nous concluons que l'accroissement de l'abondance de la lamproie en phase parasitaire est attribuable à l'amélioration de la survie des lamproies qui viennent de subir la métamorphose, ce qui est dû à la plus grande quantité des proies disponibles.
[Traduit par la Rédaction]

Introduction

The annual commercial fish yield in Lake Huron declined from 11 to 3.6 million kg from 1930 to 1966. This decline has been attributed to a combination of overfishing, habitat loss, and introduction of exotic species, such as sea lamprey (*Petromyzon marinus*) (Ebener 1995). Sea lamprey have been implicated as the most important factor reducing top predators in Lake Huron and in the other Great Lakes (Berst and Spangler 1973; Coble et al. 1990). Since 1962, federal, provincial, tribal, and state fishery management agencies in conjunction with the Great Lakes Fishery Commission (GLFC) have implemented an integrated fishery management program. This program consists of sea lamprey control and stocking and harvest management of salmonids in Lake Huron.

The GLFC initiated sea lamprey control with lampricide

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during 1960 in Lake Huron tributaries producing sea lamprey larvae (Smith and Tibbles 1980). By 1970, abundance of parasitic-phase sea lamprey in Lake Huron declined by approximately 90%. Lake trout (*Salvelinus namaycush*) stocking began in 1974, and although some fish survived and matured, natural reproduction was detected in only one area (Ebener 1995). The high mortality of lake trout prior to reproductive maturity (age 7+) has been identified as the major impediment to successful restoration. Parasitic-phase sea lamprey populations have increased dramatically in northern Lake Huron over this same period. Schleen (1992) concluded that the increase in parasitic-phase lamprey originated from the uncontrolled population of sea lamprey larvae in the St. Marys River.

In this paper, we examine three hypotheses to explain the increase in parasitic-phase sea lamprey: (*i*) an increase in sea lamprey spawning habitat in the St. Marys River resulting from coffer dam removal and flow regulation caused greater larval production; (*ii*) improvements in larval habitat quality in the St. Marys River resulting from pollution abatement resulted in greater larval production; and (*iii*) an increase in forage fish biomass and salmonid stocking in northern Lake Huron increased prey availability for parasitic-phase sea lamprey.

We compared the magnitude and timing of these changes to determine which most likely led to the historic increase in parasitic-phase sea lamprey abundance in northern Lake Huron.

Methods

We summarized data on historic patterns of sea lamprey abundance in northern Lake Huron, the north channel, and the St Marys River from 1967 to 1992. These data were examined to determine if increases in sea lamprey abundance coincided with changes in spawning and larval habitat or the abundance of forage fish.

Unpublished sea lamprey data has been deposited with the Canadian Institute for Scientific and Technical Information (CISTI)[2].

Background information

The life history of sea lamprey in the Great Lakes consists of three major stages. Larvae develop in the soft sediments of rivers over 4–7 yr (Applegate 1950; Stauffer 1962; Johnson 1969). Once larvae reach a critical size of at least 120 mm and 3 g (Homes et al. 1994), they undergo metamorphosis, during which time they do not feed. Transformers (as they are referred to) migrate to the lake where they parasitize fish for 12–18 months. Sexually mature animals return to the rivers to spawn during a 6–8 wk period in the spring and then die (Applegate 1950; Johnson 1969). Habitat requirements are distinct for each life stage of sea lamprey. Changes in habitat quantity and quality could have a significant impact on abundance and survival of subsequent life stages.

Sea lamprey were first collected in the St. Marys River in 1962 (Schleen 1992) but were probably present earlier because they were abundant in Lake Superior by the mid-1940s. Production of sea lamprey larvae may have been low from the period of colonization to 1970s because of the deterioration or destruction of spawning and larval habitat. Currently, the St. Marys River attracts more than 40 000 spawning sea lamprey each spring (Schleen et al. 1994).

The St. Marys River has been identified as an Area of Concern (AOC) by the International Joint Commission (IJC) (OMOE and MDNR 1992). It was targeted for remediation because of habitat destruction from navigation and hydro development and water-quality impairment from industrial and municipal discharges. Water and sediment quality has improved in the river since 1973, largely because of decreased industrial contaminant loadings and upgraded municipal sewage treatment plants (Kauss 1991).

Historic sea lamprey abundance patterns

Sea lamprey abundance data was available for parasitic, spawning, and larval phases. Total catch of parasitic-phase sea lamprey as a by-catch of the commercial fishery in northern Lake Huron and the north channel was available for 1967–1991. The sea lamprey management program began to purchase all parasitic-phase lamprey captured by commercial fishermen in the north channel and northern Lake Huron in 1967. The animals collected were used to determine relative abundance, sex ratio, length, weight, gut contents, location of capture, and host species, if the lamprey was attached when captured. Fishing effort was reported as the kilometres of gill net fished by those participating in the program. Effort remained relatively constant, ranging from 4000 to 6500 km of gill net per year.

Spawning-phase sea lamprey were collected annually in assessment traps fished at barriers on two streams: the St. Marys and Cheboygan rivers. Traps were checked a minimum of five times per week during the spawning runs in 1983–1993. During each check period, lamprey were enumerated and sampled for sex ratio, length, and weight. Trap efficiency and spawning run estimates were determined by mark and recapture estimates (Ricker 1975). Spawning run estimates were summed for both streams as an index of the spawning-phase cumulative run estimate.

We surveyed larval sea lamprey populations in the St. Marys River between the St. Marys rapids and Bell's Point from 1971 and 1992. This area corresponds to zones 3 and 10 from Eshenroder et al. (1987) and Kauss' (1991) zone of impaired water quality. Larvae were collected from an average of seven plots (range 2–12), each with an area of 1000 or 2000 m^2. Granular bayluside was applied at a rate of 224 $kg \cdot ha^{-1}$ through 1986 and 112 $kg \cdot ha^{-1}$ from 1987 to 1992. Two boats with two collectors per boat collected swimming larvae with scap nets for 1 h after the application of the bayluside in plots of 1000 m^2. Three boats with two collectors were assigned to the larger plots. Granular bayluside was also applied to four treatment plots with mean area of 3 ha (range 2–5 ha). Collecting procedures were similar except seven boats were used with two collectors per boat. Catch was expressed as the number of larvae collected per collector hour on the plots.

Changes in sea lamprey spawning and larval habitat

We summarized the changes in the quantity of spawning habitat in the St. Marys River as a result of instream rehabilitation efforts. Improvements in the quality of spawning and larval habitats were assessed using published data on changes in zones of impairment based on sediment contaminants and benthic communities. We compared the magnitude and timing of these habitat improvements with the increase in parasitic-phase sea lamprey populations.

Changes in the parasitic-phase sea lamprey forage base

Parasitic-phase sea lamprey feed on a variety of host species including bloater chub (*Coregonus hoyi*) and salmonids. We correlated parasitic-phase lamprey abundance with abundance and biomass of bloater chubs collected by index trawls (Argyle 1995). We also correlated lamprey abundance with Lake Huron lake trout and chinook salmon (*Oncorhynchus tshawytscha*) stocking rates (Ebener 1995). We restricted our analyses to the period from 1973 to 1992 because data were available for all time series. The series were compared using cross-correlation plots (Wilkinson 1992) and examined for significant correlations at lags ranging from –5 to 5 years.

[2] The Depository of Unpublished Data, Document Delivery (CISTI), National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

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Fig. 1. Abundance of parasitic sea lamprey collected from commercial fisher by-catch in northern Lake Huron and the North Channel, 1967–1992.

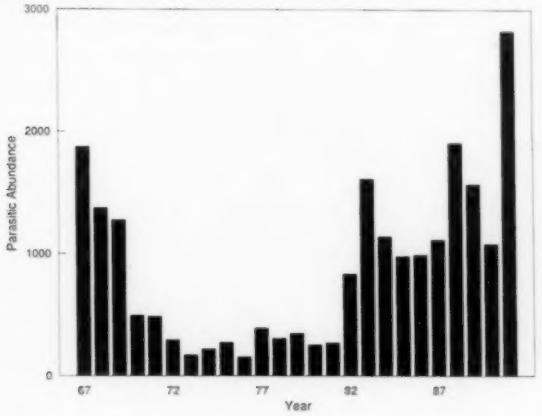


Fig. 2. The proportion of larval habitat untreated with TFM for >5 yr in all Lake Huron tributaries, excluding the St. Marys River.

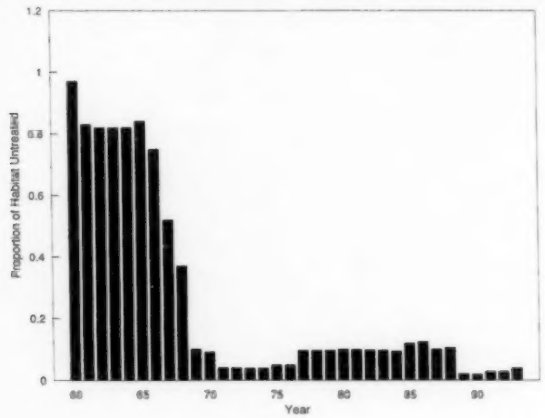
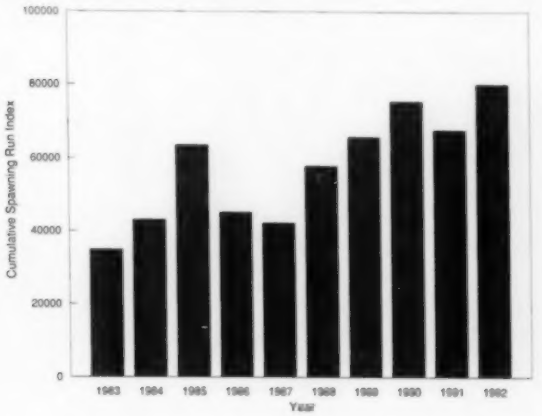


Fig. 3. Abundance of spawning-phase sea lamprey from the St. Marys and Cheboygan rivers spawning-phase assessment traps in northern Lake Huron, 1978–1992.



Results

Historic patterns of sea lamprey abundance

Sea lamprey were first collected in Lake Huron in 1937 (Applegate 1950), and by 1962 larval populations had been reported from 114 tributaries in all three basins. Abundance of parasitic-phase sea lamprey as indexed from the by-catch of the commercial fishery was high before larval control with TFM (3-trifluromethyl-4-nitrophenol) began in 1960 (Fig. 1). Streams treated with TFM before larvae metamorphose do not contribute significantly to the parasitic-phase population. On average, 5 years are required for larvae to grow to transformers in Lake Huron tributaries. Therefore, full control on Lake Huron tributaries, excluding the St. Marys River, did not occur until 1969 (Fig. 2). As a result of control efforts, parasitic-phase sea lamprey declined by more than 90%. Similar declines in lamprey populations have been observed in other Great Lakes (e.g., Hansen 1995). In lakes other than Huron, control effort has remained relatively constant and parasitic-phase abundance as indexed by spawning-phase assessment traps has stabilized at levels observed following initial control efforts. In Lake Huron, control efforts have also remained relatively stable (Fig. 2). However, parasitic-phase populations have increased significantly since 1978 and are approaching precontrol abundance in the northern main basin and North Channel (Fig. 1). This increase in the parasitic-phase population is corroborated by similar increases in catches of spawning-phase lamprey at index traps (Fig. 3).

The most significant difference between the pattern of sea lamprey control in Lake Huron and the other Great Lakes is that the channel connecting Lake Superior and Lake Huron (St. Marys River) supports a significant larval population. This population has not been controlled to date. Larval habitat within the St. Marys River accounts for greater than 65% of habitat among Lake Huron tributaries with sea lamprey populations. However, the St. Marys River could account for increased lamprey abundance in northern Lake Huron and the North Channel only if changes in lamprey habitat resulted in improved spawning success or survival of larval and parasitic-phase lamprey prior to 1977–1979.

Changes in sea lamprey spawning habitat in the St. Marys River

The St. Marys River flows 112 km from the Lake Superior outflow at Whitefish Bay to its outlet to Lake Huron. A drop of 6.7 m in elevation occurs over the length of the river, with 91% of the gradient change occurring in the St. Marys Rapids (Duffy et al. 1987). Consequently the St. Marys Rapids have the only significant accumulation of gravel and rubble suitable for sea lamprey spawning in the river (Manion and Hansen 1980; Eshenroder et al. 1987; Schleen 1992). Larval lamprey abundance may be limited by the availability of spawning habitat in the rapids because of the paucity of alternative spawning locations.

Bray (1993) documented at least 30 navigational and power generating construction events within the St Marys Rapids from 1797 to 1968. The cumulative effect of these events was a reduction of 50–60% in the rapids area resulting in a 50–90% reduction in discharge. Discharge regulation has resulted in

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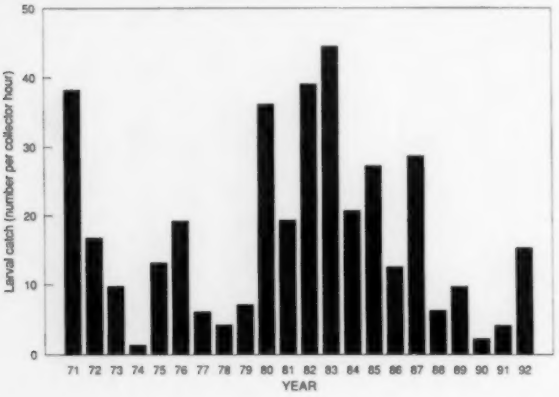
Fig. 4. Larval sea lamprey abundance in Bayer 73 surveys in the St. Marys River from the rapids to Bells Point, 1971–1992.



dewatering of the rapids for brief periods (Bray 1993). In 1982, the removal of coffer dams used in the construction of the Great Lakes Power Plant released significant quantities of spawning gravel into the Sault Basin. In addition, a berm was constructed along Whitefish Island to stabilize water flow in the St Marys Rapids and improve fishery habitat. We are not aware of published studies evaluating the impact of these two events on the quantity of potential spawning habitat. However, these changes occurred 6 or 7 yr following the increase in the parasitic-phase populations in Lake Huron. Since larvae require at least 7 yr prior to transformation in the St. Marys River (D.W. Cuddy, unpublished data), we would not expect increases in the parasitic-phase population resulting from spawning habitat improvements until 1989. Therefore, changes in spawning habitat likely did not significantly contribute to increased parasitic-phase populations in northern Lake Huron.

Changes in sea lamprey larval habitat in the St. Marys River

The potential larval habitat in the St. Marys River is estimated to be 6700 ha (Eshenroder et al. 1987). The capacity to produce sea lamprey larvae may have been impaired by degraded water and sediment quality. Elevated bacterial levels indicating degraded water quality have occurred since at least 1904 (Kauss 1991). Sediment contaminants exceeding the Ontario Ministry of the Environment (OMOE) and IJC guidelines include phenols, wood particles, cyanide, metals (iron, zinc, chromium, copper, lead, mercury), oil and grease, and polychlorinated biphenyls (PCBs) (OMOE and MDNR 1992). Sediment cores from Little Lake George show that concentrations of polycyclic aromatic hydrocarbons (PAHs), zinc, and oil and grease occurred between the mid-1960s and mid-1970s (UGLCCS 1989; Kauss 1991). Subsequent controls have resulted in a substantial decline in sediment contamination (Kauss 1991).

Kauss (1991) and Burt et al. (1991) mapped zones of impairment in the St Marys River based on sediment concentrations of oil and grease and zinc, as well as benthic community structure. These analyses indicate that the areas of impairment are concentrated along the Canadian shore from the Algoma Steel Corp. ship dock (slag pile) to the head of Little Lake George. The benthic invertebrates in this area are dominated by the pollution-tolerant oligochaetes, *Tubifex tubifex* and *Limnodrilus hofmeisteri* (Kauss 1991). Despite declines in sediment contamination, benthic invertebrate community structure indicated that a zone of moderate to severe impairment persisted to Little Lake George at least until 1985.

Peaks in abundance of larval sea lamprey were observed in 1971 and 1983, both before and after reported declines in sediment contamination could have influenced larval populations (Fig. 4). The magnitude of variation was high, and although the frequency of higher catches increased during the 1980s, no trend in abundance was evident.

The limited spatial scope of changes in larval habitat quality in the St. Marys River could not account for the three- to five-fold increase in parasitic-phase sea lamprey abundance. Comparing the larval habitat (Eshenroder et al. 1987) with the degraded zone mapped by Kauss (1991) and Burt et al. (1991) demonstrates that the degraded area represents only 6% of the larval habitat and 17% of the river's lamprey productive capacity. It is unlikely that full recovery of this zone could account for the magnitude of increase in sea lamprey abundance in northern Lake Huron and the North Channel.

Parasitic-phase sea lamprey and prey fish interactions

An increase in the abundance indices of (*i*) parasitic-phase sea lamprey abundance, (*ii*) the biomass of bloater chub, (*iii*) lake trout stocking rates, and (*iv*) chinook salmon stocking rates from 1973 to 1991 is shown in Fig. 5. Sea lamprey and bloater chub biomass were cross-correlated at lags ranging from -3 to 3, indicating that both series have similiar, significant trends (Wilkinson 1992). The highest correlation occured at lag 0 ($r = 0.83$, $p < 0.05$). These data indicate that sea lamprey abundance is significantly correlated with the current year's bloater chub biomass. Bloater chub sampled in the fall show considerable wounding and recently transformed sea lamprey attached to bloater chub are common in the Detour Channel, northern Lake Huron (Fleischer 1993).

Lake trout stocking rates were also significantly correlated with lamprey abundance at lag 4+ ($r = 0.50$, $p < 0.05$). Lake trout are stocked as yearlings; therefore, parasitic-phase lamprey abundance was correlated with age 5+ lake trout. Ebener (1995) reported that age 5+ lake trout have the highest incidence of lamprey wounds. Similarly, parasitic-phase abundance was significantly correlated with ages 1+ to 4+ chinook salmon. The highest correlation ($r = 0.63$, $p < 0.05$) occurred with age 3+ chinook salmon. Again, Ebener (1995) reported the highest incidence of wounding on age 3+ chinook.

These data indicate a significant correlation between abundance of parasitic-phase lamprey and the abundance of prey species. An increase in food availability could result in improved survival of recently metamorphosed and parasitic-phase sea lamprey. The recovery of spawning-phase sea lamprey marked as transformers increased from 0.05% in 1965–1967 to 2.9% in 1978–1979 and 8% in 1992 (Bergstedt and Seelye 1995; R. Bergstedt and L. Hansen, U.S. National Biological Service, unpublished data), indicating that transformer survival increased significantly during the study period.

Bloater chub biomass increased by approximately 60 times

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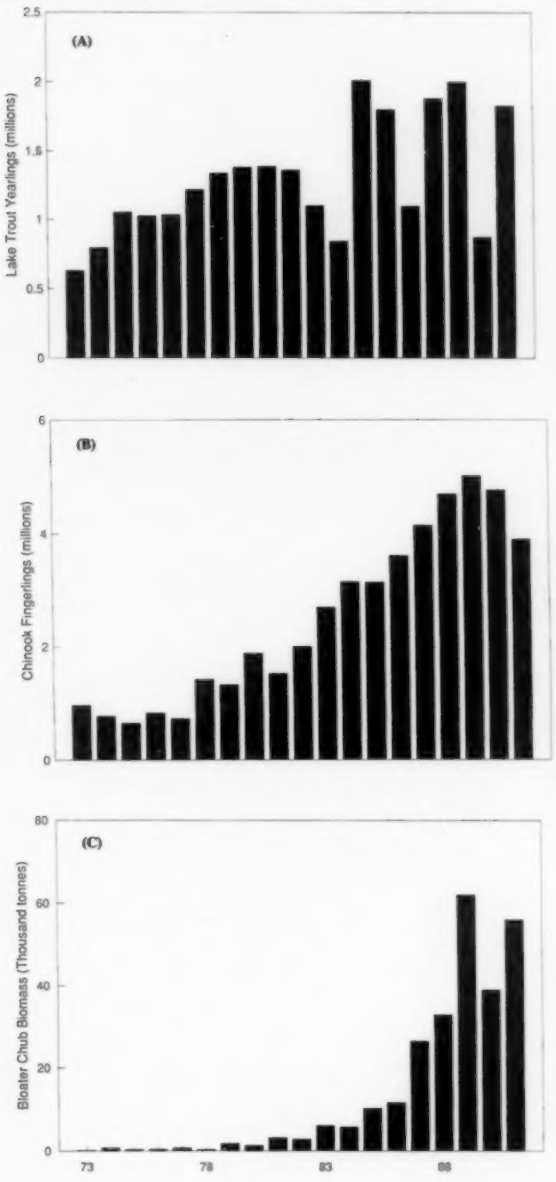
Fig. 5. Changes in (A) lake trout yearling stocking, (B) chinook salmon fingerling stocking, and (C) bloater chub biomass, 1973–1991 (from Ebener 1995).



coincident with the increase of 3–5 times in the parasitic-phase sea lamprey abundance. Stocking rates for chinook salmon fingerlings and lake trout yearlings increased from 800 000 to 4 000 000 and from 1 000 000 to 3 000 000, respectively. The timing of increases in prey fish coincides with the increases in parasitic-phase abundance. These data support the hypothesis that the increase in parasitic-phase sea lamprey was due to an increase in prey abundance.

Discussion

The recent increases in parasitic-phase sea lamprey abundance in northern Lake Huron originated from the St. Marys River. Control effort in the remaining Lake Huron tributaries has remained similar to those in other Great lakes where lamprey abundance has remained low or has been further depressed. Because the St. Marys River contains nearly 66% of lamprey-producing habitat, the river has the potential to support precontrol levels of parasitic-phase populations in northern Lake Huron. However, we found little evidence to support habitat remediation as the primary cause of the increase in sea lamprey numbers.

Although the number of spawning-phase lamprey increased in the St. Marys River (as in the Cheyboygan River) there was no significant increase in larval abundance over the same time period. Thus, historic declines in spawning habitat and recent efforts to prevent dewatering of fish habitat in the St. Marys River could not account for the increase in parasitic-phase lamprey abundance.

Larval habitat in impaired areas of the St. Marys River has improved since at least 1971. Concentrations of most significant contaminants have decreased as a result of pollution-abatement programs. Despite these declines, benthic communities have not fully recovered. The continued presence of significant areas of contamination may account for the relatively stable production of larval sea lamprey throughout the study period. In addition, the majority of the area inhabited by larval sea lamprey is outside the impaired area. The possible improvement in habitat could not account for the size of the parasitic-phase increase.

Our data indicate that the increase in parasitic-phase sea lamprey in northern Lake Huron was likely due to an increase in prey availability. Survival from metamorphosis to parasitic feeding is a critical stage in the life cycle of sea lamprey. During metamorphosis, lamprey do not feed and utilize a significant proportion of lipid reserves. Condition factor can decline from 1.6 at the beginning of transformation to 1.3 when transformation is complete (Potter et al. 1978). Potter (1980) reported that recently metamorphosed sea lamprey from the St. John's River utilized most of their lipid reserves and began protein catabolism if they were unable to feed on upstream migrating teleosts. Swink (1995) found feeding and water temperature to be critical to survival of transformers during their first winter in the lake. Johnson and Anderson (1980) reported that 63% of newly transformed (<200 mm) juveniles were captured by the Lake Superior and Lake Michigan deepwater cisco fisheries. Transformers from the St Marys River have been reported to feed heavily on bloater chub in spring and early summer (Ebener 1995). The pattern of bloater chub abundance was significantly related to parasitic-phase abundance both following initial control in Lake Huron and during the more recent increase.

We also observed a significant relation between parasitic-phase sea lamprey abundance and salmonid stocking rates. Houston and Kelso (1991) reported significant positive relations between parasitic sea lamprey weight and sex ratio with food availability (as indexed by salmonid stocking rates). We conclude that the stocking of lake trout and chinook salmon may have inadvertently supported increases in parasitic-phase sea lamprey populations in northern Lake Huron. However,

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the rehabilitation of reproducing populations of lake trout in northern Lake Huron is dependant on suppression of production of larval sea lamprey in the St. Marys River.

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Restoration of Lake Erie: contribution of water quality and natural resource management

Joseph F. Koonce, W.-Dieter N. Busch, and Thomas Czapla

Abstract: Since the 1960s, the open-water fish community of Lake Erie recovered dramatically, partly as a result of water-quality and natural-resource management initiatives (including reduction in loadings of phosphorus and toxic contaminants, promotion of wetland protection, restriction of commercial fishing, and implementation of quota management for walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*)). Reviews of historical changes reveal complex interactions of overexploitation of fishery resources, invasion of non-indigenous species, eutrophication, extensive habitat modification, and toxic contamination. Native fish species that required tributary or neashore habitat for spawning and nursery areas have declined markedly. Among surviving native species, such as walleye, stock diversity declined with the loss of tributary spawning stocks and lake spawning stocks became dominant. With the rarefaction of native species, abundance of formerly subdominant species or opportunistic, non-indigenous species increased. Species such as smelt (*Osmerus mordax*), gizzard shad (*Dorosoma cepedianum*), and white perch (*Morone americana*) have less dependence on critical tributary and nearshore habitat. In this paper, we evaluate whether the shifts in fish community structure in Lake Erie reflect the elimination of tributary and wetland habitat. Major unresolved issues are the extent to which habitat loss inhibits recovery of native species associations and the sufficiency of management coordination to identify and restore critical habitat.

Résumé : Depuis les années 1960, la communauté ichtyenne des eaux libres du lac Érié s'est rétablie de façon exceptionnelle, en partie à cause des mesures prises pour améliorer la qualité de l'eau et la gestion des ressources naturelles (notamment une réduction du phosphore et des contaminants toxiques, la promotion de la protection des milieux humides, les restrictions en matière de pêche commerciale et la mise en oeuvre de contingents pour le doré et la perchaude). Les études qui ont porté sur les changements survenus dans le passé ont révélé des interactions complexes entre la surexploitation des ressources halieutiques, l'invasion d'espèces non indigènes, l'eutrophisation, la modification considérable de l'habitat et la contamination par des matières toxiques. Parmi les espèces de poissons indigènes, celles qui ont besoin d'habitats dans des affluents ou près du rivage pour la fraye et l'alevinage ont considérablement diminué. Chez celles qui ont survécu, tel le doré, la diversité des stocks a diminué avec la perte des stocks de géniteurs provenant des affluents, au profit de ceux du lac. Avec la raréfaction des espèces indigènes, on a observé une augmentation des espèces non indigènes, jadis subdominantes et opportunistes. Des espèces comme l'éperlan, l'alose à gésier et le baret n'ont pas un besoin vital des habitats situés dans les affluents et près du rivage. Dans le présent article, nous examinons si les changements intervenus dans la structure de la communauté ichtyenne du lac Érié peuvent être corrélés à l'élimination des habitats des affluents et des milieux humides. Parmi les principaux points qui restent à résoudre, signalons l'absence de données permettant de déterminer à quel point la perte d'habitats empêche le rétablissement des associations d'espèces indigènes, et le manque de coordination au niveau de la gestion pour déterminer quels sont les habitats vitaux et de quelle façon on pourrait les remettre en état.
[Traduit par la Rédaction]

Introduction

Lake Erie is a recovering ecosystem. According to Hartman (1973), the degradation of the fish community of Lake Erie reached its most extreme level in the 1960s. The combined effects of eutrophication, overexploitation of fishery resources, extensive habitat modification, and pollution had severely changed the entire Lake Erie ecosystem. Commercial fisheries experienced declines in preferred species and harvests reflected a progressive decline in lake trout (*Salvelinus namaycush*), lake herring (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), sauger (*Stizostedion canadense*), and blue pike (*Stizostedion vitreum glaucum*) and increasing reliance on less preferred species (Leach and Nepszy 1977). By the late 1960s, the last remaining native predator, the walleye (*Stizostedion vitreum vitreum*), had fallen to a low level. Beginning in the 1970s, fishery management strategies and pollution abatement programs contributed to a dramatic reversal. Lake Erie walleye fisheries rebounded to world-class status (Hatch et al. 1987), and point-source phosphorus loading has declined to target levels in the 1972 Great Lake Water Quality Agreement (Dolan 1993). Associated with these reductions in phosphorus loading were a dramatic decrease in the abundance of nuisance and eutrophic species of phytoplankton (Makarewicz 1993*a*) and an decline in zooplankton biomass (Makarewicz 1993*b*). Surveys of the benthic macroinvertebrate communities further illustrate the improvement in the most degraded sediment areas of western Lake

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Erie. Compared with surveys conducted in 1969 and 1979, Farara and Burt (1993) found that there was a marked decline in the abundance of pollution tolerant oligochaetes and that overall the macroinvertebrate community of western Lake Erie shifted to more pollution intolerant and facultative taxa.

The invasion of zebra mussels (*Dreissena polymorpha*) into Lake Erie has affected this recovery trend. Leach (1993) reported that, associated with zebra mussel increases between 1988 and 1991, water transparency increased 77%, chlorophyll *a* decreased 60%, and number of zooplankters declined 65%. Although Leach (1993) observed an increase in *Gammarus* in nearshore benthic communities dominated by zebra mussels, Dermott (1993) has observed an inverse relation to abundance of *Diporeia* and the quagga mussel (*Dreissena bugensis*). These changes in water quality and associated plankton and benthic communities make predictions about future status of the Lake Erie ecosystem highly uncertain. Recent trends show declines in abundance of smelt (*Osmerus mordax*), white perch (*Morone americana*), yellow perch (*Perca flavescens*), and walleye with increase in abundance of lake whitefish. Understanding these changes requires separation of cause-effect linkages among pollution reduction, exploitation, and habitat modification.

This paper evaluates the effects of these ecosystem changes and associated water-quality and fish-management initiatives on changes in the structure of the fish community in Lake Erie. Specifically, we formulate and explore a hypothesis that habitat degradation is the primary organizing factor underlying changes in fish community structure. In habitat degradation, we consider chemical loadings, which lead to changes in water quality, and nearshore and tributary habitat alterations, which lead to changes in the physical structure of critical spawning and nursery habitat.

Methods

We obtained data for this paper primarily through historical sources. Catch records from commercial fisheries were the main source of information about changes in the fish community of Lake Erie (Baldwin et al. 1979) from 1900 through the 1970s. The Great Lakes Fishery Commission (M. Dochoda, personal communication) maintains these summaries by distributing reports of Lake Committees for each of the Great Lakes. The Lake Committee reports also include reports of harvest by sports fisheries as well as results of various, ongoing assessment studies. We also relied on reports of walleye and yellow perch task groups of the Lake Erie Committee for virtual population reconstructions from catch data (Knight et al. 1994; Dietz et al. 1993). To develop profiles of habitat preferences of selected fish species, we drew upon a report by Hartley and Herdendorf (1977), an expansion on this report in Herdendorf et al. (1992), and narrative summaries of Trautman (1981) and Scott and Crossman (1973).

The documentation of the history of nutrient and toxic contaminant loadings is widely available. In addition to many literature sources, we relied extensively on recent reports of the governments of the United States and Canada that were distributed for the 1994 State of the Lakes Ecosystem Conference, SOLEC (Environment Canada and U.S. Environmental Protection Agency 1995). We found the history of habitat modification more difficult to reconstruct and relied on another of the SOLEC reports (Dodge and Kavetsky 1994) and other literature sources to generate a profile of habitat changes.

Results and analysis

In examining changes in commercial fish production between 1900 and 1965, Beeton (1969) noted the nearly simultaneous demise of the fisheries for sauger, whitefish, blue pike, and walleye from 1955 to 1960. This period also included the first reported extensive oxygen depletion and changes in the benthos of Lake Erie. Concern with the deteriorating condition of Lake Erie, in fact, had led the governments of Canada and the United States in 1964 to refer the matter to the International Joint Commission (IJC) under the provisions of Article IX of the Boundary Waters Treaty of 1909. The governments were convinced that these changes were caused by pollution from sewage and industrial wastes. In the popular press, this was the time of the "death" of Lake Erie.

In 1969, an IJC report (Campbell et al. 1969) found that all major sources of pollution contributed directly or indirectly to the degraded condition of Lake Erie, Lake Ontario, and the international section of the St. Lawrence River. Of the problem areas identified, eutrophication emerged as the dominant threat to the Lake Erie ecosystem. The role of phosphorus in stimulating excess algal growth had been well established (Campbell et al. 1969), and the effect of the excess production on oxygen demand in the sediments of the lake was cause for concern. Hartman (1973) reported that periods of low dissolved oxygen were a major problem in Lake Erie, with the elimination of mayflies (*Hexagenia*) being an indication of the severity of the problem. The rate of oxygen depletion had apparently increased by the early 1950s. In 1953, a period of calm, hot weather caused sufficient stratification for the bottom waters of the western basin of Lake Erie to fall below 1 $mg \cdot L^{-1}$. This level proved fatal for mayfly nymphs. Mayflies did not recover and by the early 1960s were absent from the benthos that they once dominated.

With the 1972 Great Lakes Water Quality Agreement, Canada and the United States sought to lower phosphorus loading. The agreement had three main objectives: (*i*) eliminate nuisance algal growth in Lake Erie, Lake Ontario, and the International Section of the St. Lawrence River; (*ii*) restore year-round aerobic conditions to the hypolimnion of the central basin of Lake Erie; and (*iii*) maintain the oligotrophic condition of the upper Great Lakes.

Fish biologists were also concerned about patterns of anoxia in the central basin hypolimnion. Regier and Hartman (1973) argued that the central basin hypolimnion may have gone anoxic for the first time in the mid-1950s. Anoxia in the hypolimnion, therefore, was associated prominently with the demise of blue pike, which reached greatest abundance in the deep waters of the central and eastern basins of Lake Erie. The goal of restoring year-round aerobic conditions to the central basin became a necessary condition to restore the habitat for fish, and the governments of Canada and the United States set a target phosphorus load of 11 000 t yr^{-1} to achieve this goal (Vallentyne and Thomas 1978). Bertram (1993) found evidence that that total phosphorus concentrations and oxygen depletion rates in the central basin of Lake Erie are decreasing in response to these loading reductions, but Charlton et al. (1993) also showed that resilience of the offshore of the central basin seems to make it less responsive to nutrient reductions than nearshore areas or the western basin.

Understanding of the relation between phosphorus loading and incidence of anoxia in the hypolimnion of the central basin has changed since the setting of targets for phosphorus loading. Charlton (1980) first noted that, when oxygen depletion

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Fig. 1. Mean monthly water levels for Lake Erie from 1900 to 1990. Data are courtesy of the Great Lakes Environmental Research Laboratory.

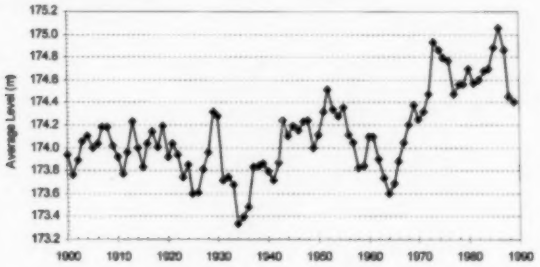
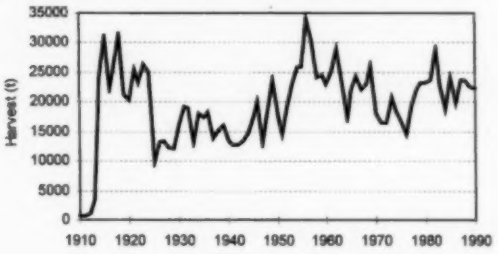


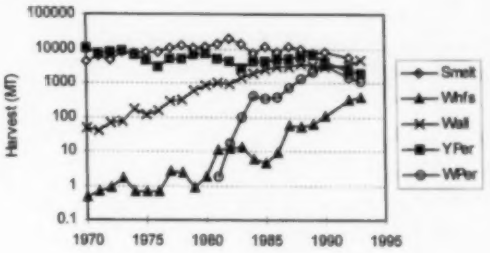
Fig. 2. Trends in commercial harvest, 1910–1990 (after Baldwin et al. (1979) and data from the Great Lakes Fishery Commission).



rates are corrected for hypolimnion thickness and temperature, there appears to be no historical trend in the rate of oxygen depletion (hence probability of anoxia) from the 1930s to the 1970s. Reynoldson and Hamilton (1993) further reported that, from profiles of mayfly tusks in sediment cores of Lake Erie, periods of anoxia occurred prior to European colonization. El-Shaarawi (1987) related the probability of anoxia in the central basin to the joint effect of climate and phosphorus loading. Climatic factors affect the temperature of the hypolimnion and the mean water level of the lake. As Charlton (1980) noted, hypolimnion temperature is a function of weather conditions during the spring, but water level fluctuations have long-term periodicities (Fig. 1). From this vantage point, it is not surprising that the 1960s was a period of poor water quality in Lake Erie. Water levels in 1962 were among the lowest on record (Fig. 1), and through much of the 1960s low water levels were characteristic of Lake Erie. Thus, even without elevated phosphorus loading, there would have been a higher probability of anoxia in the central basin hypolimnion.

Eutrophication was not the only concern of fish biologists. Analyses of the changes of the fish community (Hartman 1973; Regier and Hartman 1973; Leach and Nepszy 1977) revealed a number of possible causes: overexploitation, watershed and shore erosion, nutrient loading, introduction of toxic materials, invasion of new species, and stream and wetland destruction. Leach and Nepszy (1977) argued that the commercial fishery through overexploitation was the dominant stress leading to the declines of lake trout, lake herring, sauger, blue pike, walleye, and yellow perch and that the major concern for the immediate future was the regulation of exploitation.

Fig. 3. Total harvests of selected species: smelt, lake whitefish (Whfs), walleye (Wall), yellow perch (Yper), and white perch (WPer) (after Baldwin et al. 1979 and data from the Great Lakes Fishery Commission).



The decline and recovery of walleye was the prime example of the importance of overexploitation. After the extinction of blue pike, walleye harvests also began to decline (Hartman 1973). Through the 1960s, walleye abundance fluctuated about low levels until the discovery of mercury contamination, which resulted in closure of the walleye fishery (Leach and Nepszy 1977). With the closure of the walleye fishery, fish management agencies began to limit exploitation. The walleye recovery in Lake Erie most certainly results from the aggressive regulation of fishing mortality imposed by a quota management strategy (Hatch et al. 1987). Prior to the closure of the fishery, J.H. Kutkuhn (unpublished data, available from the Great Lakes Fishery Commission, Ann Arbor, Mich., Scientific Protocol Committee Report on western Lake Erie walleye, submitted to the Lake Erie Committee June 1976) estimated that walleye older than 1.5 yr had annual mortality rates of 90%. Under quota management, mortality rates dropped to 30% (Hatch et al. 1987). The walleye recovery was dramatic. Hatch et al. (1987) report that angling catch rates rarely exceeded 0.1 walleye per angler hour during the 1950s and 1960s. By 1975, these catch rates had risen to 0.61 walleye per angler hour, and there followed a dramatic increase in sports harvests and sports fishing effort.

Although the historical variation of walleye abundance is consistent with changes in exploitation, other changes in fish community structure in Lake Erie are difficult to reconcile primarily with either effects of pollution or commercial fisheries. As Leach and Nepszy (1977) noted, commercial fisheries have fluctuated about a long-term average of 20 000 t from 1915 to 1993 (Fig. 2). Since 1970, smelt and yellow perch have been major components of the commercial harvest. The contribution of these two species, however, has declined while other species have increased (e.g., walleye, white perch, and lake whitefish; Fig. 3).

The response of these five species is not as expected if pollution (particularly eutrophication) and overexploitation were the dominant and controlling stresses on the fish community. Fish managers lowered fishing mortality on walleye and then yellow perch through implementation of quota management. Water-quality management produced declining phosphorus loading. The effects of these management actions are in conflict. Lowered fishing mortality should result in higher abundance of yellow perch and walleye. Lowered nutrient loading should decrease primary production, which limits growth and reproduction of walleye, yellow perch, and other

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Fig. 4. Abundance estimates of walleye and yellow perch in Lake Erie from 1978 to 1994. Virtual population estimates for yellow perch are after Dietz et al. (1993) and for walleye, after Knight et al. (1994).

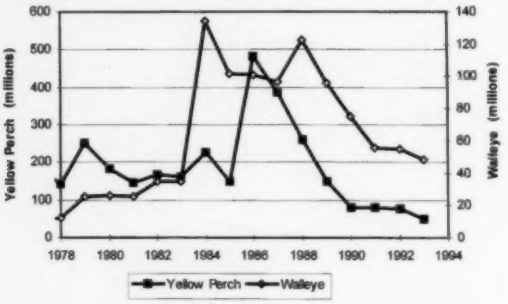
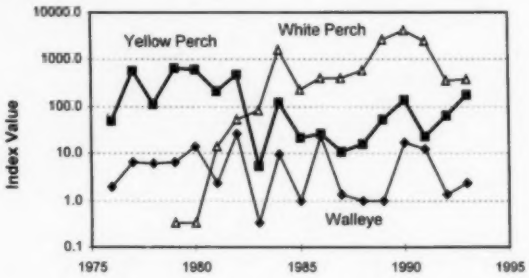


Fig. 5. Trends in relative abundance of age-0 walleye, yellow perch, and white perch in Ohio waters of Lake Erie, 1976-1993. Data are averages of index values for Districts 1, 2, and 3. Index values are based on fall trawl surveys conducted by Ohio Department of Natural Resources.



species. In concert, therefore, these actions should result in greater abundance of adult fish, having lower growth rates, and a decrease in recruitment, caused both by decreased productivity and by increased predation on juveniles.

Fish species did not respond to these changes in management actions as expected. Lake whitefish increased in reported harvests by commercial fishing while smelt yields decreased in recent years (Fig. 3). Both walleye and yellow perch populations increased dramatically in the early 1980s (Fig. 4), but both populations later declined. Trawl surveys of young-of-the-year reveal that walleye and yellow perch had variable recruitment from 1976 to 1993 with a slight downward trend (Fig. 5). In contrast, white perch recruitment increased from the early 1980s to 1990 until it began declining through 1993 in parallel with declining harvests in the commercial fishery. Because these five species function quite differently in the Lake Erie fish community, ecological interactions may explain these varied responses to reduction in nutrient loading and quota management of the fisheries. Nevertheless, it is difficult to reconcile these varied responses with simple cause-effect hypotheses involving the direct effects of quota management on yellow perch and walleye and of reduction of phosphorus loading.

A more general review of changes in diversity of Lake Erie fish indicates that other factors may have caused the instability of the fish community. Van Meter and Trautman (1970) document observations of 138 fish species in Lake Erie and its tributaries. Commercial fishing records are available for 35 of these species and 19 species have contributed significant harvests (Hartman 1973). In Table 1, we present a summary of information on 35 species for which sufficient evidence exists to compare their origins, spawning habitat requirements, and changes in abundance. This summary draws upon a report by Hartley and Herdendorf (1977), an expansion on this report in Herdendorf et al. (1992), and work by Trautman (1981) and Scott and Crossman (1973). Six of the 35 species in Table 1 are non-indigenous, including goldfish (*Carassius auratus*), carp (*Cyprinus carpio*), gizzard shad (*Dorosoma cepedianum*), smelt, alewife (*Alosa pseudoharengus*), and white perch. Using these sources, we assigned a relative abundance rank for both the period prior to 1800 and current conditions: abundant, common, rare, extinct (or extirpated), and not present. We also summarized spawning habitat preference for tributary or nearshore habitat and the specificity of habitat preference. We assigned a low habitat specificity (L) to those species that spawn in a variety of habitat types and high specificity (H) to species with a narrow preference range for physical features of spawning habitat.

The change in the species composition of Lake Erie is associated with a decline in abundance of species that have narrow preferences for spawning habitat (Table 1). Of the 11 species that we now judge to be common or abundant, 5 are non-indigenous with low specificity for spawning habitat. We judged that 16 of the species had low specificity for spawning habitat. Native species included in this list were quillback (*Carpiodes cyprinus*), largemouth bass (*Micropterus salmoides*), emerald shiner (*Notropis atherinoides*), northern pike (*Esox lucius*), muskellunge (*Esox masquinongy*), black bullhead (*Ameiurus melas*), yellow bullhead (*Ameiurus natalis*), brown bullhead (*Ameiurus nebulosus*), sauger (*Stizostedion canadense*), walleye, and lake whitefish. Of these, three have recently increased (walleye, lake whitefish, and black bullheads). As discussed by Trautman (1981), the inverse abundance relationship between black and both brown and yellow bullheads is related to habitat degradation. Of the remaining species, esocids (muskellunge and northern pike) and centrachids depend as adults upon nearshore habitat with submerged aquatic vegetation. Quillback remained stable and the decline of emerald shiner seems unrelated to spawning habitat. Therefore, we propose that degradation of spawning and nursery habitat in tributaries and the nearshore environment of Lake Erie has contributed to the decline of many native species (lake sturgeon (*Acipenser fulvescens*), several cyprinids, white sucker (*Catostomus commersoni*), and lake herring) and remains an obstacle to their recovery.

Habitat degradation does not always limit production of species with high specificity for spawning habitat. The critical determinant of limitation is not the absolute amount of habitat, but amount of habitat relative to habitat requirements of all life-history stages of a species (cf. Minns 1995). Although we lack the level of detail necessary to characterize fully the spawning and nursery habitat requirements of Lake Erie fish species, we found ample reason to pursue an expansion of Table 1. Fish community structure of Lake Erie depends upon the biological diversity of its fish species, and variability of life-history expression reflects the biological diversity of each

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Table 1. Summary of characteristics of selected species of Lake Erie fish.

Species name	Common name	Origin[a]	Spawning		Abundance	
			Location[b]	Specificity[c]	Pre-1800	Now
Carassius auratus	Goldfish	NI	T,N	L	NP	C
Cyprinus carpio	Common carp	NI	T,N	L	NP	A
Dorosoma cepedianum	Gizzard shad	NI	T,N	L	NP	A
Osmerus mordax	Rainbow smelt	NI	T,N	L	NP	C
Alosa pseudoharengus	Alewife	NI	T,N	L	NP	C
Morone americana	White perch	NI	T	H	NP	A
Acipenser fulvescens	Lake sturgeon	N	T	H	C	R
Carpiodes cyprinus	Quillback	N	T,N	L	R	R
Catostomus commersoni	White sucker	N	T	H	C	R
Lepomis gibbosus	Pumpkinseed	N	N	H	C	R
Lepomis macrochirus	Bluegill	N	N	H	C	R
Micropterus dolomieui	Smallmouth bass	N	N	H	C	R
Micropterus salmoides	Largemouth bass	N	T,N	L	C	R
Pomoxis annularis	White crappie	N	N	H	C	C
Pomoxis nigromaculatus	Black crappie	N	N	H	R	R
Notemigonus crysoleucas	Golden shiner	N	T	H	C	R
Notropis atherinoides	Emerald shiner	N	N,O	L	C	R
Notropis hudsonius	Spottail shiner	N	N	H	C	R
Pimephales notatus	Bluntnose minnow	N	T	H	C	R
Pimephales promelus	Fathead minnow	N	T	H	R	R
Esox lucius	Northern pike	N	T,N	L	C	R
Esox masquinongy	Muskellunge	N	T,N	L	C	R
Ameiurus melas	Black bullhead	N	T,N	L	R	C
Ameiurus natalis	Yellow bullhead	N	T,N	L	C	R
Ameiurus nebulosus	Brown bullhead	N	T,N	L	C	R
Ictalurus punctatus	Channel catfish	N	T	H	C	R
Morone chrysops	White bass	N	N	H	A	R
Perca flavescens	Yellow perch	N	N	H	A	C
Stizostedion canadense	Sauger	N	T,N	L	C	E
Stizostedion vitreum glaucum	Blue pike	N	?	?	A	E
Stizostedion vitreum vitreum	Walleye	N	T,N	L	C	C
Coregonus artedii	Lake herring or cisco	N	N	H	A	R
Coregonus clupeaformis	Lake whitefish	N	T,N	L	C	R
Salvelinus namaycush	Lake trout	N	N	H	C	R
Aplodinotus grunniens	Freshwater drum	N	N	H	A	A

[a]N, native species; NI, non-indigenous species.

[b]T, tributary; N, nearshore; O, open lake.

[c]L, low; H, high.

[d]A, Abundant; C, common; R, rare; E, extinct or extirpated; NP, not present.

species. Walleye, for example, spawn in rivers and spawning reefs, and these spawning preferences are the basis of walleye subpopulation structure in Lake Erie. This biological diversity of walleye provides the means of escaping limitation due to degradation of tributary spawning habitat by dams, siltation, and other tributary modifications. Nevertheless, the relative absence of reef habitat in the central basin limits the productivity of central basin walleye more than in the western basin. In losing nearshore and tributary habitat, the structure of the Lake Erie fish community continues to be driven by the most opportunistic species. The dominance of non-indigenous species in Lake Erie thus could be due more to habitat degradation than to overexploitation and nutrient enrichment.

Because habitat degradation and alteration is the least understood of the major stresses acting on the Lake Erie ecosystem, rigorous testing of this hypothesis is not possible. Although the importance of physical and chemical habitat to lake productivity has long been recognized (e.g., Rawson 1939), the complexity of these interactions and their effects on community structure and function remains a barrier to developing a workable system for inventory and classification of Great Lakes habitat (Herdendorf et al. 1992). Nevertheless, the losses of nearshore and tributary habitat of Lake Erie due to human activities has been major:

(*i*) Loss of coastal wetlands. Through drainage and infilling, the extensive wetlands of the western basin have been reduced. The Black Swamp in the Maumee River drainage basin, for example, has been reduced from 4000 to 100 km^2 (Dodge and Kavetsky 1994). Of the remaining coastal wetlands, nearly all are diked to provide protection from wave

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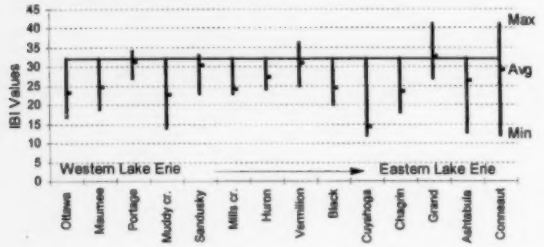
Fig. 6. Minimum, maximum, and mean index of biotic integrity (IBI) for 14 estuaries. For comparison the Warm Water Habitat aquatic life use criterion value of 32 is plotted as a solid line (WWH Criterion). Figure is from R.F. Thoma (Ohio Environmental Protection Agency).



action (Bookhout et al. 1989). The remaining undiked wetlands are often degraded by erosion and siltation (Prince et al. 1992).

(*ii*) Loss of tributary habitat. The 21 tributaries have been subjected to extensive modification, including dams, channelization, dredging to maintain navigation channels, hardening of the shorelines of the estuarine reaches with rip-rap and bulkheads, and erosion and sedimentation due to bank destabilization in upper reaches.

(*iii*) Loss of rocky shorelines. The nearshore of Lake Erie has been extensively modified with groins, jetties, and breakwaters, which have altered natural shore processes of erosion and deposition (Carter 1973). The shifting of unstable substrates creates barrier beaches and zones of erosion where more resistant substrates become exposed. Much of the Lake Erie shoreline is composed of beach. Exposed rocky substrates are thus threatened by altered patterns of erosion and deposition as well as by the spread of zebra mussels (Dodge and Kavetsky 1994).

The significance of this loss of habitat is suggested by the loss of fish species diversity (Table 1). R.F. Thoma (Ohio Environmental Protection Agency, Columbus, Ohio, unpublished data) found that the degradation of the biological integrity of the estauarine portions of Ohio's tributaries to Lake Erie was severe (Fig. 6). Using an Index of Biotic Integrity, Thoma found that only one of the 14 estuaries met minimal integrity standards. Factors responsible for the degraded conditions included extensive habitat modification, loss of wetlands, point source discharges, and non-point-source pollutants. The remaining habitats are critically imperiled. Despite government commitments to "no net loss of aquatic habitat," conversion of natural habitats for agricultural, urban, or industrial uses continues (Dodge and Kavetsky 1994). Protection of remaining coastal wetlands through diking preserves wetland habitat for wildlife and migrating waterfowl, but not for fish. Furthermore, diked wetlands become extremely vulnerable to long-term changes in water level. The present system of dikes and distribution of coastal wetlands arose in a period of high water levels. Koonce and Hobbs (1994) reasoned that the patchwork pattern of preserved wetland areas may be insufficient for adaptation to changing regimes of water levels that will be associated with future climate change. The coastal development of Lake Erie thus limits the capacity of natural shorelines to adapt to changing flow and water level regimes in a way that minimizes additional damage to fish and wildlife populations.

Discussion

On a lakewide basis, regulation of pollution and regulation of fisheries have been the basis of Lake Erie management. There is no doubt that sewage effluents, industrial discharges, and excessive fishing have contributed to the degradation of the fish community of Lake Erie. However, invasion of non-indigenous species and habitat degradation severely limit its biological recovery (Koonce 1994). In fact, we find sufficient evidence to hypothesize that habitat alteration fundamentally entrained the extent of change in the structure and function of the Lake Erie fish community.

The current fish community of Lake Erie represents a balance of stresses and recovery transients. Summarizing the effects of management activities on trends in fish community structure, we find the following:

(*i*) Exploitation is now regulated. The value of the fisheries may fluctuate with the abundance of desired species, but targeted species remain vulnerable. Fishery landings, while variable, continue to provide harvests commensurate with historical averages. Commercial fishery is now focused on small-bodied animals and non-indigenous species are a major component of the harvest. Angling is similarly opportunistic with the result that fishery management adapts to constraints imposed by invasions of non-indigenous species and habitat loss.

(*ii*) Eutrophication is now less of a threat. Phosphorus loadings have declined to target levels, and there is new concern that Lake Erie's central and western basins are in transition from mesotrophy to oligotrophy and eutrophy to mesotrophy, raising the question whether fish species are limited now more by productivity or habitat. A transition in ecosystem function is taking place, but fish community may lack the species diversity to respond to benthic-based food webs that are being created by the invasion of zebra mussels.

(*iii*) Contaminants remain a problem in that they seem to have stabilized at a level sufficient to warrant concern. Given the growing significance of atmospheric sources, there seems to be little expectation of change. In fact, there may follow a slight increase in body burdens of some organochlorine compounds with additional complication of food webs.

Invasion of non-indigenous species and habitat loss are largely unregulated. Prevention measures taken by governments (such as adopting balast discharge regulations) reduce these stresses, but these efforts have neither the scale of effort nor resources that have been devoted to regulation of exploitation and chemical pollution. This imbalance of approach seems curious in retrospect. Invasion of exotic species and habitat disturbance are linked, and we believe that a new framework is needed to manage habitat protection and restoration.

Herdendorf et al. (1992) reviewed the physical and chemical basis for classification and inventory of Great Lakes habitat. Their approach to habitat classification linked morphometry to community structure and function. We suspect that the key to understanding changes in the fish community of Lake Erie requires understanding the effects of habitat alteration on the success of individual fish species. Diversity

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of a fish community, its structure, and its function depend first on the availability of species that are capable of completing their life cycle within the lake ecosystem. Species vary, however, in their attributes and contribution to community structure and function. Current declines in smelt and white perch populations may represent a shift in the food web of Lake Erie resulting from the invasion of zebra mussels. Energy flow seems to be channeled more to the benthos, and planktivory as a feeding niche will become less productive. Historically, macroinvertebrates such as mayflies were an important component of the food web, and though species characteristics are quite different, we see a return to a benthic-based food webs in Lake Erie. Many of the historically important fish species in Lake Erie, however, are now limited by availability of spawning and nursery habitat, and non-native species such as white perch and smelt do not seem sufficiently adaptable to fill this benthic feeding niche.

We suggest that understanding the historical changes in the fish community of Lake Erie and its future restoration will depend upon a clearer perspective on styles of use of habitat by fish. For example, there is new concern over the limitation of phosphorus loading for Lake Erie with the invasion of zebra mussels (Neilson et al. 1994). The basic question is whether phosphorus reduction now imperils the productivity of the Lake Erie fish community. Addressing this issue requires determining whether productivity is limited by habitat or by nutrient loading. If managers accept the premise that, due to habitat constraints, a planktivory-based fish community is the choice of fishery managers, then the system may indeed be limited by nutrient loading. Should the habitat constraints be removed from fish populations, which can utilize benthic-based food webs more effectively, then managers might find fish production less dependent on nutrient loading. We believe that the loss of so many native species and their failure to recover is a manifestation of habitat limitation.

Water quality and fishery management have approached restoration of Lake Erie from different perspectives. Obvious problems have been corrected, but Lake Erie remains a highly stressed ecosystem. It seems time to ask fundamental questions about why Lake Erie is so vulnerable to disruption by the invasion of exotic species. The zebra mussel invasion has radically altered energy flow and nutrient cycling dynamics in Lake Erie. Ruffe (*Gymnocephalus cernuus*) invasion and expansion in Lake Superior threatens yet another major challenge to the Lake Erie ecosystem (Dodge and Kavetsky 1994). Existing independence of management of water quality, fishery resources, and even water quantity seems no longer productive or sufficient to deal with emerging challenges of ecosystem management. Lakewide management plans (LaMP) offer an opportunity for unification of approaches.

Within the framework of the Joint Plan for the Strategic Management of Great Lakes fisheries (SGLFMP), Lake Erie fish managers are attempting to develop a set of Fish Community Objectives (FCO) that will guide future management actions. They are also required to develop a set of complementary Environmental Objectives that specify the environmental characteristics necessary to achieve the FCOs. As set forth in the 1987 Protocol for the Great Lakes Water Quality Agreement, water-quality managers are committed to developing Ecosystem Objectives for each of the Great Lakes and to restoring their beneficial uses. Environmental Objectives of the fish managers could be useful benchmarks for the water-quality managers in their determination of restoration of beneficial uses. This overlap of common interests, however, depends upon reconciling FCOs and Ecosystem Objectives. Clearly, this reconciliation must involve an integration of plans for the development of nearshore environments. The Lake Erie LaMP offers the opportunity for discussion of these issues, but the technical foundations of these discussions will require a more careful consideration of the linkage between physical habitat and stable life-history patterns among fish species. Derivation of something like a habitat guild concept would be an important step in completing the kind of classification and inventory system propose by Herdendorf et al. (1992). With such a system in place, derivation of specific Environmental Objectives for Lake Erie will be placed on a firmer scientific foundation.

Acknowledgment

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Assessment of habitat impairments impacting the aquatic resources of Lake Ontario

W.-D.N. Busch and S.J. Lary

Abstract: A habitat classification system was used to describe aquatic habitat and evaluate habitat degradation in Lake Ontario. Primary consideration was given to physical loss or disruption of habitat availability; because habitat availability was treated as a functional entity, disruptions or stresses caused by chemical or biological sources were included. Data on biological, chemical, and physical anthropogenic changes were scattered, patchy, and disjointed. Therefore, the Delphi technique was used to evaluate the degree of functional habitat impairment for 29 habitats. The criteria for the impairments were the severity of the ecological impact (shift in trophic transfer efficiency) and its permanence (short > decades > permanent). The amounts of functional degradation were averaged by habitat categories ($N = 88$) for each habitat and multiplied by the estimated areal proportion of that habitat in the ecosystem. We estimated that during 1970–1990, Lake Ontario's ecosystem health was degraded by 58%. Impairments were caused almost equally by anthropogenic stresses from biological (loss of indigenous and introduction of exotic species), chemical (persistent toxins), and physical (dredge–fill, damming, and water-level regulations) sources. Our finding is consistent with a late 1980s study that used lake trout (*Salvelinus namaycush*) as an indicator of ecosystem health.

Résumé : Nous avons appliqué un système de classement des habitats à la description d'habitats aquatiques dans le lac Ontario et à l'évaluation de leur détérioration. Nous nous sommes occupés surtout de la destruction physique ou de la perte d'utilisation d'habitats; puisque les habitats utilisables sont traités sous l'angle d'entités fonctionnelles, nous avons inclus tout stress ou source de perturbation d'origine chimique ou biologique. Les données sur les changements physiques ou biochimiques d'origine anthropique étaient éparses, fragmentaires ou inordonnées. C'est pourquoi nous avons eu recours à la technique Delphi pour l'évaluation de la détérioration du fonctionnement de 29 habitats. Les critères retenus étaient la gravité de l'impact écologique (changement observé en termes d'efficacité des transferts trophiques) et sa durée (courte durée, dJcennies, caractère permanent). Nous avons calculé la moyenne par catégorie d'habitats ($N = 88$) du degré de détérioration des habitats étudiés sur le plan de leur fonctionnement, et multiplié le résultat obtenu par le pourcentage de la superficie estimée que cet habitat occupe dans son écosystème. Nous avons estimé qu'entre 1970 et 1990, l'écosystème global du lac Ontario s'est détérioré de 58 %. Les sources de détérioration, d'importance sensiblement égale, étaient les stress anthropiques à caractère biologique (perte d'espèces indigènes et introduction d'espèces exotiques), chimique (substances toxiques persistantes) et physique (dragage/remplissage, endiguement et régulation du niveau de l'eau). Nos observations confirment les résultats d'une étude faite à la fin des années 1980 qui utilisait le touladi comme indicateur de l'état des écosystèmes.
[Traduit par la Rédaction]

Introduction

A restoration or rehabilitation activity requires an understanding of the impairments to an ecosystem or the cause of deviation from the "healthy" state (Evans et al. 1990; Environment Canada and U.S. EPA 1995). Some efforts have been made to evaluate the state of the Lake Ontario ecosystem (Christie et al. 1986; LOPCHIC 1993). The overall decline in condition and its present degraded state has been documented. However, the specific condition indicators, such as changes in fish and wildlife species diversity, harvest rates, nutrient abundance, chemical loadings, human population growth, land clearing, and shoreline modifications, have not been measured consistently, and the data have not been evaluated holistically (Christie 1973; Crowder and Painter 1991; Luckey 1994; Hartig and Law 1994).

The Great Lakes Water Quality Agreement (GLWQA 1987) states that "impairment of beneficial use(s) means a change in the chemical, physical, or biological integrity of the Great Lakes System sufficient to cause any of the following (italics added for emphasis):

(1) restrictions on fish and wildlife consumption;

(2) tainting of fish and wildlife flavor;

(3) *degradation of fish and wildlife populations*;

(4) *fish tumors or other deformities*;

(5) *bird or animal deformities or reproduction problems*;

(6) *degradation of benthos*;

(7) restrictions on dredging activities;

(8) *eutrophication or undesirable algae*;

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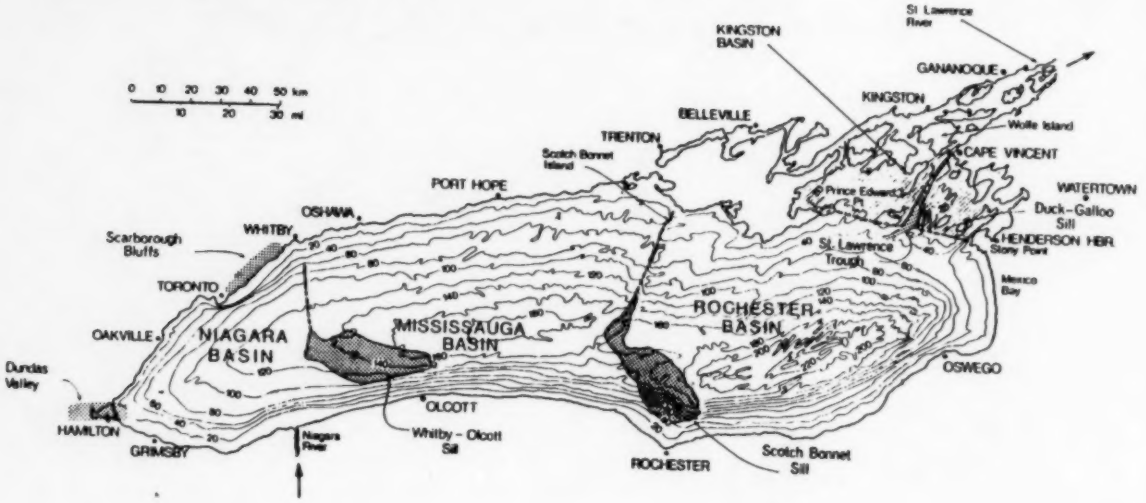
Fig. 1. Lake Ontario basins (modified from Sly and Prior 1984).



(9) restrictions on drinking water consumption, or taste and odor problems;

(10) beach closings;

(11) degradation of aesthetics;

(12) added costs to agriculture or industry;

(13) *degradation of phytoplankton and zooplankton populations*; and

(14) *loss of fish and wildlife habitat*."

Some of the criteria listed above are stand-alone measurements of impairment. However, criteria 3, 4, 5, 6, 8, and 13 are subsets or symptoms of criterion 14 if habitat is defined as the biological, chemical, and physical setting needed to support all life functions of the organisms (Sly and Busch 1992*a*). Therefore, anthropogenic chemical, physical, or biological stressors may disrupt the integrity of the system through impairments to ecosystem functions, such as trophic transfer. These impairments to the health of the ecosystem are in addition to the more commonly identified, acute effects caused when habitats are physically destroyed (Sly and Busch 1992*a*).

Along these lines, this study assessed the functional impairments to the habitats of the Lake Ontario ecosystem in terms of anthropogenic changes to chemical, physical, or biological integrity (GLWQA 1987; Environment Canada and U.S. EPA 1995). Data on physical changes to the basin were identified and inventoried. Information on chemically caused stresses were reviewed. The biological impacts caused by exotic species on the health of the ecosystem were also evaluated. The results from these assessments were combined to obtain an index of ecosystem health for Lake Ontario. This index can be used as a tool for understanding the specific impairments to the ecosystem and to assist in the development of concise, achievable restoration options for the ecosystem.

Geographic area and hydrology

Lake Ontario, with a surface area of 19 010 km^2, is the smallest of the Laurentian Great Lakes (Fig. 1). Its longest dimension, in an east–west direction, is approximately 306 km. The width is about 85 km. The mean depth is 84 m, while maximum depth is 245 m. Despite the small surface area, Lake Ontario is the twelfth largest lake in the world by volume.

Lake Ontario is divided into four basins. The three major basins, the Niagara, Mississauga, and Rochester, going from west to east, are separated by the Whitby–Olcott and Scotch Bonnet sills, respectively. The easternmost basin, the Kingston, is separated from the Rochester basin by the Duck–Galoo sill.

The sediments follow a gradient of sands and gravels in the nearshore areas to silts and clays in the deeper portion of the basins. The Niagara basin has a maximum depth of 128 m, while the Mississauga basin's maximum is about 201 m deep, and the Rochester basin's maximum depth is approximately 245 m. The Kingston basin has a maximum depth of 30 m. Islands and extensive littoral areas are common in the Kingston basin (Eckert 1984; Martini and Bowlby 1991; Sly 1991).

Lake Ontario receives the outflow from the upper four Great Lakes via the Niagara River at the average annual rate of 5520 $m^3 \cdot s^{-1}$. Direct inflow from all other major tributaries total only an additional 540 $m^3 \cdot s^{-1}$ (Sly 1991). Despite the lake's great depth, the theoretical water retention time is only 6 yr because of the high inflow from the Niagara River (IJC 1989). Fluctuations in the water level of Lake Ontario are less than 2 $m \cdot yr^{-1}$, far less than historical fluctuations (Sly 1991). This is largely a result of artificial water-level regulation coupled with a relatively small surface area, which limits evaporation effects.

Limnology and biota

Lake Ontario is a dimictic lake, undergoing vernal and autumnal mixing. Summer stratification results in classical zonation.

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Winter stratification is rather weak since the lake usually remains free of ice, with the exception of inshore shallow areas and sheltered embayments. Hypolimnetic upwellings are common, even during maximum summer stratification (Johannsson and O'Gorman 1991). Vertical thermal bars are a feature of the warming and cooling processes of the lake and serve to temporarily segregate inshore and offshore waters, particularly at the outset of summer stratification. The isolation of inshore waters serves to restrict dispersion of nearshore pollutants, nutrients, and other loadings (Eckert 1984). Circulation is typically wind driven, and is frequently of several cells, corresponding generally with the sub-basins.

The period of time that was examined for this study (1970–1990) was one of significant and rapid change in water quality and in species composition, abundance, and condition (Smith and Lange 1994). However, it was also a period of relative stability in the physical attributes of the basin (Whillans et al. 1992). Most tributary damming for hydro-power production had occurred prior to 1970, although these dams still prevent up- or down-stream movement of biota. The rate of other shoreline alterations such as shoreline protection, dredging, or filling decreased, in part due to restrictions caused by governmental regulations.

Until the middle to late 1980s, the trophic status of Lake Ontario was considered mesotrophic based on average phosphorus concentrations (IJC 1989; Leach and Herron 1992). Yet, many inshore areas and embayments were decidedly eutrophic. The phytoplankton community of Lake Ontario was dominated (90%) by diatoms, green algae, dinoflagellates, and flagellates. *Cladophora* sp. was the predominant attached algae. The zooplankton community was dominated by *Bosmina longirostris* and *Daphnia retrocurva* (Johannsson and O'Gorman 1991). *Diporeia hoyi* and *Mysis relicta* dominated the deepwater benthos, while the more eutrophic, nearshore regions were predominantly occupied by oligochaetes, particularly *Potamothrix sp.* and *Aulodrilus sp.*

Fish species in the epilimnion, in order of numerical abundance, were alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), yellow perch (*Perca flavescens*), white sucker (*Catostomus commersoni*), and lake chub (*Couesius plumbeus*) (LOPCHIC 1993; Smith and Lange 1994). Alewife, rainbow smelt, and slimy sculpin (*Cottus cognatus*) dominated the deep waters (Jones et al. 1993). Native lake whitefish (*Coregonus clupeaformis*) abundance was very low. Top cold-water predators were hatchery supported populations of rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), Pacific salmon (*Oncorhynchus sp.*), and a limited number of Atlantic salmon (*Salmo salar*). Embayments supported local populations of northern pike (*Esox lucius*), largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), yellow perch, white perch (*Morone americana*), and brown bullhead (*Ameiurus nebulosus*) (Eckert 1984).

Commercial harvest was limited by management regulations and species availability during 1970–1990. Catches were chiefly catfish (*Ictalurus sp.*), bullhead, walleye (*Stizostedion vitreum*), white perch, American eel (*Anguilla rostrata*), and, by the late 1980s, included increasing numbers of lake whitefish (Eckert 1984; IJC 1989; Sly 1991). During this time, a very active offshore sports harvest had been established. The harvest included exotic and native salmon and trout.

In the late 1980s to early 1990s, the return to more natural conditions in water quality caused changes in primary and secondary production, and consequently in the fish community (Smith and Lange 1994). Significant reductions in the artificially high levels of nutrients, as a result of improved sewage treatment, combined with the changes in energy flow caused by the zebra mussel (*Dreissena polymorpha*), reduced primary productivity in the "open waters" (Smith and Lange 1994; Environment Canada and U.S. EPA 1995). Consequently, the trophic status of Lake Ontario's fish community shifted from mesotrophic to oligotrophic (Jones et al. 1993; Smith and Lange 1994). The primary forage species, the exotic alewife, appeared to be declining in both abundance and condition (Jones et al. 1993). Yet, native fish species such as lake whitefish and burbot (*Lota lota*) increased greatly in abundance and efforts to reestablish naturally reproducing lake trout are showing signs of success. For example, 1995 offshore stock assessment by New York State Department of Environmental Conservation and the National Biological Service indicated that the 1994 year class of lake trout in Lake Ontario included 8% naturally produced fish (C. Schneider, New York State Department of Environmental Conservation, personal communication).

Methods

Definition of aquatic habitat(s)

In classical biological usage, habitat is generally described as a geographical entity, such as a coastal marsh or the littoral zone of a lake. Little emphasis is placed on other life-support functions needed by the biota (Cowardin et al. 1979) and, therefore, lacks the focus needed for a detailed analysis and evaluation of the functional health of a complex, multiple habitat ecosystem. Margalef (1981) and Ryder and Edwards (1985), for example, have identified the need for a more functional ecosystem-based approach to habitat evaluation, especially from a management viewpoint. A process using a functional-based habitat application was recently provided by Sly and Busch (1992*a*). Under this approach, habitat is defined as the sum total of the biological, chemical, and physical attributes of a specific location, which constitutes a distinct fish or wildlife refuge, feeding site, or breeding location.

For the current project, habitat units were described and assigned biological, chemical, and physical descriptors to provide the means for evaluation of the availability and functional health of these habitats (Busch et al. 1993). A list of impairments, with descriptors, was also developed (Busch et al. 1993). These are stresses (biological, chemical, or physical) that interfere with the normal functions of the habitat unit and, therefore, affect life processes of organisms living within that habitat unit.

Habitat classification methodology: identification and justification

The Aquatic Habitat Classification System (AHC) was used to inventory and assess the Lake Ontario ecosystem. The complete methodology is described in Busch and Sly (1992). The selection of potential habitat units was based on well-defined physical factors, such as topography, stratigraphy, and other classical landform descriptors. These habitats were then considered from the perspective of biological interactions and community structure, whether actual or potential.

The habitat information inventory available from Busch et al. (1993) provided the habitat information base and a list of functionally distinct habitat units. The information and supportive literature were identified, obtained, and organized according to its biological, chemi-

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Fig. 2. The hierarchy of aquatic habitat classification.

Sub-System[1] ⟶	Division ⟶	Sub-Division	Class[2]				
			Wc	Wq	S	Pm	Pc
Open water		Deep water reef, > 25 m	✓		✓		
Circulatory basin		Fluvial deposition zone	✓		✓	✓	
	Open water	Major embayment, < 25 m deep	✓		✓	✓	
		Major embayment, > 25 m deep	✓		✓		
		Relict trench	✓		✓	✓	
		Sub-basin, < 25 m	✓		✓	✓	
		Sub-basin, > 25 m	✓		✓		
Nearshore		Active sand dune	✓		✓		✓
	Shoreline	Erodible bluff	✓		✓		✓
	Shoreline & littoral zone < 3 m	Erodible plain	✓		✓		✓
		Non-erodible bluff	✓		✓		✓
		Non-erodible plain	✓		✓		✓
		Relict sand dune	✓		✓		✓
		Upland			✓		✓
	Wetlands	Open water, connected		✓	✓	✓	✓
		Not connected		✓	✓	✓	✓
	Tributary & embayments	Embayment, restricted	✓		✓	✓	✓
		Embayment, tributary dominated	✓		✓	✓	✓
		Embayment, unrestricted	✓		✓	✓	✓
		Tributary reach	✓	✓	✓	✓	✓
	Special features	Artificial fill / breakwall			✓		✓
		Artificial island			✓		✓
		Artificial shoal, < 25 m	✓		✓	✓	
		Artificial spit / jetty			✓		✓
		Barrier structures			✓		✓
		Offshore bar / lagoons	✓		✓	✓	✓
		Pond	✓		✓	✓	✓
		Rocky outcrop	✓		✓		✓
		Shoal / Reef, < 25 m	✓		✓	✓	

Water column = Wc Water quantity = Wq Substrate = S Plant material = Pm Plant cover = Pc

[1]AHC System after Sly and Busch (1992b)

[2]Each Class level descripter had three modifiers - biological, chemical, and physical.

cal, and (or) physical application. An "expert system" or Delphi technique (Zuboy 1981; Crance 1987) was used to evaluate the anthropogenic stresses to determine major impairments to habitat functions.

Applying the AHC hierarchy as a model, all lake habitats fall under two major categories, or subsystems (Fig. 2). The open water subsystem includes the circulatory basins and major embayments and extends shoreward to either the sand–silt sediment boundary or the attached plant boundary, whichever reaches the greater depth. Shoreward of this boundary is the nearshore subsystem that includes all coastal features as well as islands and shallow water features such as reefs and shoals. These are included here since they, like the shore, are dominated by edge or interface effects.

The nearshore subsystem area from the shore to the 25-m contour constitutes a separate zone from deeper waters. This is based on the following criteria: (*i*) wave activity exerts its influence to a maximum depth of approximately 25 m (Sly 1991), and (*ii*) thermocline development in Lake Ontario is restricted to the top 25 m (Sly 1991). Thus, the major, wind-driven physical forces defining this habitat exert their effects above the 25-m contour.

The nearshore subsystem is described from a classical geological basis. Since subsequent definitions of habitat units rely on an understanding of coastal morphology, the following definitions were adopted. The shore is that zone from the low-water mark landward to the base of a cliff, large or small, which marks the landward limit of effective wave action. A cliff, in this sense, refers to the abrupt change in gradient, no matter how small, indicating where wave erosional forces cease, and is usually demarcated by a change in vegetation and substrate. Wetlands are described by Cowardin et al. (1979).

Criteria to evaluate stresses on aquatic habitats

Criteria were developed from literature sources and from consultations with natural resource managers to evaluate stress (Busch et al. 1993). The goal was to identify and describe stress factors capable of impairing the functions performed by a habitat unit in support of

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Table 1. Estimated anthropogenic impairments (stresses) affecting habitat functions in Lake Ontario.

Habitats combined by general categories[a]	Biological stresses	Chemical stresses	Physical stresses	Total stress impact by habitats
Open water (67%)	0.11	0.03	0.02	0.16
Shoreline (100 m inland) and littoral area (3 m) (15%)	0.03	0.03	0.03	0.09
Wetlands (4%)		0.01	0.02	0.05
Tributary and embayments (12%)	0.04	0.09	0.12	0.25
Special features (2%)	0.01	0.01	0.01	0.03
Total stress impact by type	0.21	0.17	0.20	0.58

Note: Habitats were combined into five general categories. Estimated impact was multiplied by its estimated percent of total surface area for watershed effect.

[a]Values in parentheses are the percentage of the basin surface area for each category.

fish or wildlife in the Lake Ontario basin. From this information, criteria were established to assess the degree of degradation of specific habitat units (Schindler 1987).

The evaluation of the degree of habitat degradation (biological, chemical, and physical) necessitated several considerations. After a specific habitat unit was delineated, the degree of impairment was determined using the Delphi technique (Zuboy 1981; Crance 1987). An effort was made to separate the natural from the anthropogenic restrictions. The functional concerns were addressed by comparing impacted areas to reference sites within the basin that have maintained their structure and are able to support ecosystem functions needed for a healthy state (Martin 1994).

Functional impairments of 88 habitat categories (class level; Sly and Busch 1992*b*) were evaluated for biological, chemical or physical stresses. The criteria were the severity of the ecological impact, defined as a significant change or shift in the efficiency or direction of the energy flow between trophic levels, and the expected permanence of the stress defined by time (weeks, season, year, decades, or permanent). The application of the Delphi technique to the assessment used a scale of 0.1 to 1.0 to estimate the degree of disturbance for each of the two criteria and the 88 habitat categories (Fig. 2). The assessment process was repeated and applied to address the biological, chemical, and physical stress factors causing functional impairments. The results were combined and averaged for five habitat groups and were multiplied by an approximation of the size of the habitat's area (percentage of the water-surface area of the system) to relate the impairment to the total health of the ecosystem.

Procedure for the inventory of aquatic habitat information

The aquatic habitat data are from Busch et al. (1993). The data were obtained in 1991–1992. The information search was not restrained by information type, format, source, or national borders. It included raw data, scientific papers and reports, interviews, office visits, and information requests using all applicable media.

Ideally, assessment of ecosystem condition should focus, like a snapshot, on a narrow time period. The length of time allowed for the assessment window is especially relevant if the system is going through major changes. Throughout the information gathering phase, it became increasingly clear that Lake Ontario habitat information was scattered, patchy, and disjointed. Some portions of the lake system have been studied in detail, while other areas have not been studied. Therefore, to obtain the best applicable understanding, a lengthy time frame was allowed, 1960–1990, with the major focus on the 1970–1990 period.

Results

The results indicate that the habitats making up the Lake Ontario ecosystem, during the 1960–1990 (focus 1970–1990), were functionally impaired by 58% (Table 1). The impairments were caused almost equally by biological (21%), chemical (17%), and physical (20%) stressors.

Biological stresses were most severe in the open water habitat category, which comprises 67% of the basin's surface area. Its functional performance was determined to be impaired by the dramatic increase in distribution and abundance of exotic species, most notably the sea lamprey (*Petromyzon marinus*) and zebra mussel (Environment Canada and U.S. EPA 1995). Other contributing factors included artificial changes in primary production and instability within the native fish community caused by loss of native species such as lake trout, Atlantic salmon, blue pike (*Stizostedion vitreum glaucum*), and deepwater sculpin. This change in the open-water community and the loss of native species resulted in management agencies stocking Lake Ontario with exotic predator species to provide fishing opportunities and to control the high production of exotic prey species. The wide geographic and trophic distribution of the exotics and their permanence resulted in the high stress indicator (Table 1).

Chemical stresses were highest in the tributary and embayments habitat category (Table 1). Most of the larger tributaries and embayments are also harbors with extensive shoreline development and historic chemical loadings, with high levels of point and nonpoint contributions (Rang et al. 1992; Luckey 1994). Some of these areas have been labeled Areas of Concern as a result of determinations that their degraded state is impacting the lake–ecosystem. The impacts include fish tumors, wildlife deformities, and degradation of aquatic biota caused by chemical accumulation from the sediments or watershed (Hartig and Law 1994; Koonce et al. 1996).

Physical stresses were primarily from physical and waterflow changes caused by hydro-power development, construction of harbor facilities, and maintenance dredging for harbors in the tributaries (Smith 1995). They, combined with the chemical stresses, resulted in the finding of the tributary and embayments habitat category as the most heavily stressed habitat type of Lake Ontario (Table 1).

Surprisingly, shoreline–littoral and wetland habitats were not identified as being heavily stressed habitats during the study period (Table 1). This was partially the result of the time frame; governmental regulations for protection of lake-connected wetlands and the shoreline and littoral zone have strengthened so that the physical area of these habitat units had not decreased significantly in the last 20 yr. Prior to government restrictions, shoreline–littoral and wetland habitats were

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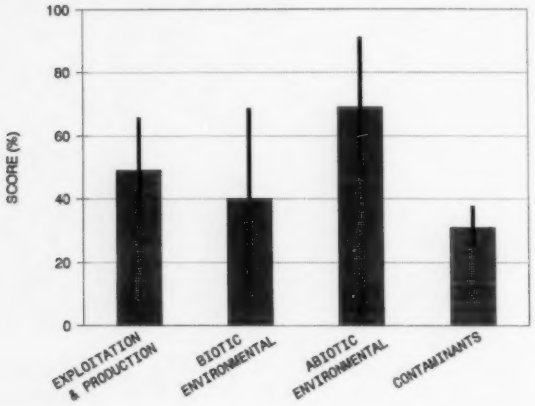
Fig. 3. Dichotomous key scores, by stress category, for Lake Ontario. The vertical line extending from each bar indicates percent uncertainty (from Edwards et al. 1990).



greatly altered. In addition to agriculture, extensive urbanization, particularly in the vicinities of Toronto, Hamilton, and Rochester, has significantly impacted the shoreline and associated wetlands. Local loss of urban wetlands is estimated to be greater than 80%, with an overall total loss of 50% (Whillans et al. 1992).

Discussion and recommendations

The impacts by society on the Lake Ontario ecosystem have been severe. The aquatic resources are impaired and anthropogenic stresses continue to have significant negative impacts on the ecosystem (Colborn et al 1990; EOWG 1990; IJC 1989; LOPCHIC 1993; Luckey 1994; Environment Canada and U.S. EPA 1995). The estimated overall impairment reported in Table 1 is very similar to the health condition of 50% reported for Lake Ontario by Edwards et al. (1990). Their results described the conditions in the mid-1980s using a dichotomous key, with lake trout as the index species (Ryder and Edwards 1985; Ryder 1990; Marshall, Ryder, and Edwards 1992). Edwards et al. (1990) include "exploitation and production" as a significant stressor since their assessment focused on lake trout performance (Fig. 3). Conversely, in our aquatic habitat assessment, the focus was on the impairments to the functional performance of the habitats. Both this and the Edwards et al. (1990) ecosystem health assessments indicate that the chemical stresses in Lake Ontario, although still of concern, are less important than the physical and biological impairments, which are the most significant restoration impediment.

The goal of restoration of the Lake Ontario ecosystem is the same as that defined in the GLCPA (1990) for the entire Great Lakes system: "of restoring and maintaining the chemical, physical, and biological integrity of the waters of the Great Lakes Basin." Furthermore, the specific requirement for implementation of lakewide management plans (LaMPs) in GLCPA (1990) mandate "a systematic and comprehensive ecosystem approach to restoring and protecting the beneficial uses of the waters." Protection of the beneficial uses of these waters is also required by the Boundary Waters Treaty (1909), and restoration is the goal of the GLWQA (1987).

Yet, anthropogenic impacts on Lake Ontario's ecosystem health must be factored into restoration planning. Historical conditions or natural, undisturbed ecosystems are often suggested as targets or examples of ecosystem restoration benchmarks. This would appear applicable when humans are not a major component of the landscape. However, in ecosystems such as Lake Ontario where continuing human development is a major factor, humans have to be considered part of the landscape (Geller 1994). The use of undisturbed systems, or the predevelopment time frame, as comparison for today's anthropogenically stressed systems, undermines the ecosystem approach by excluding the avoidable and unavoidable impacts of humans within that landscape.

The current challenge for natural resource managers is to understand the ecosystem's functional vitality within its structure, the interactions between trophic levels, and the effects of human use of the ecosystem on its restoration (Kerr 1974; Borgmann 1982; Sprules and Munawar 1986; Environment Canada and U.S. EPA 1995). The identification of obstructions to the functional vitality, for example, through disruptions in the energy flow by zebra mussels, is fundamental to assessing ecosystem vitality and the functional impairments caused by anthropogenic stresses (Rapport 1990; Steedman and Regier 1990). A focus on the ability to support "biological functions" allows for natural and (or) anthropogenic changes in species assemblages within an ecosystem that could still be described as "functionally healthy" even though stressed, for example, by extensive harvest (Schindler 1987; Ryder and Kerr 1990).

Although a general ecosystem health assessment of Lake Ontario that describes an impaired system has been conducted, more data are needed to monitor and evaluate rehabilitation progress. The selection of data and geographic coverage should focus on the scale and specificity needed for the project. The detailed data collection could follow an organizational structure like that provided by the AHC, so that the information can be added to that available for improved system understanding and cost effectiveness.

Based on our review of the state of the Lake Ontario information, priority areas include the following.

(1) Protect the system from unintentional introductions or invasions of nuisance exotic species and limit the impacts of the exotic species already present.

(2) Assess impairments to structure and productivity of the open-water biological resources by the following. *(i)* Continuing a bioindex program to collect lakewide lower trophic level data on total phosphorous, chlorophyll *a*, and zooplankton to describe spatial and temporal changes. The information will verify the accuracy of the nutrient loading objectives and allow improvements in the management of sustainable fish production. *(ii)* Assessing the strength and health of the fish community using a trophic and habitat guild approach to identify the effectiveness of habitat utilization. This activity should also identify the potential carrying capacity at the various trophic levels and estimate the differences between actual use and potential (Czapla et al. 1995).

(3) Identify, quantify, remediate, and monitor the physical

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and chemical impairments to biological functions in tributary–embayment habitats (Table 1), including the following. *(i)* Continue the progress for migratory, tributary fish to regain up- and down-stream passage and access to up steam habitats. *(ii)* Continue the remediation of impairments caused by chemicals accumulated in the sediments or watershed through regulatory processes so that fish and wildlife can safely occupy the tributary–embayment habitats. Obtain, through index organisms, data on normal background levels of natural chemicals and the frequency of deformities, at the whole, reproduction, cellular, and DNA level, to differentiate anthropogenic-caused stresses from those naturally occurring.

(4) Develop a computerized data base with a Geographic Information System to fully integrate available information into a concise model of the Lake Ontario habitat inventory.

While some historical impacts are reversible (i.e., toxic contaminant loading, excessive nutrients, overharvesting), others are not (i.e., exotic species introductions, drainage basin changes, native species extirpation). To implement ecosystem management, "desired" natural resource goals need to be identified and understood (Evans et al. 1990; Bertram and Reynoldson 1992). Society within the Lake Ontario basin is now debating the natural resource goals for this system. Although the theoretical options range from "a return to pristine conditions" to "intense aquaculture" (put–grow–take), neither extreme can be reached or sustained because of irreversible anthropogenic changes or economic limitations. There are a range of options in restoration initiatives to reach ecosystem goal(s), but these options need to be described so that society can evaluate the benefits. Ecosystem health models can clarify the options and benefits (Minns 1992). The information obtained from ecosystem health assessments provides a focus for action in restoring the health of the lake by assisting in identifying and ranking the numerous stresses affecting the system. This information is useful in recognizing the most significant problem (stress) areas and providing guidance for more detailed and quantifiable evaluations. Such a focus assists in improving the cost effectiveness of efforts towards rehabilitation of not only the Lake Ontario ecosystem but other aquatic systems as well.

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Rates of natural and anthropogenic change in shoreline habitats in the Kingston Basin, Lake Ontario

A.A. Crowder, J.P. Smol, R. Dalrymple, R. Gilbert, A. Mathers, and J. Price

Abstract: Shoreline habitats in the Kingston Basin have experienced continual change on a wide range of time scales, as a result of physical, chemical, and biotic stresses of both natural and anthropogenic origin. Not all change can or should be controlled. From a management perspective, stresses can be usefully subdivided into those that originate from the lake as a whole (e.g., water-level and-chemistry changes, introduction of exotic species) and those originating from the adjacent land area (e.g., point-source contamination and sedimentation). Stresses from the lake cannot be controlled locally, whereas those arising from terrestrial activities are more easily managed. Slow rates of change are less likely to have dramatic effects than rapid change, but a small change can have catastrophic effects if it exceeds the threshold tolerance of an ecosystem. Dramatic alterations to the entire ecosystem can also occur if a single, important species (e.g., a macrophyte) is adversely affected, because of complex feedback responses between the various components of the system. Thus, management strategies should focus on those areas that are particularly susceptible to land-based stress and on stresses that are most likely to exceed the tolerance of key components of an ecosystem.

Résumé : Les habitats des rivages du bassin de Kingston ont connu des changements continuels pendant une vaste gamme d'échelles temporelles à cause d'agressions physiques, chimiques et biotiques d'origine naturelle et humaine. Toutefois, il n'est pas possible ou souhaitable de limiter tous ces changements. Sur le plan de la gestion, on peut subdiviser utilement ces stress en deux catégories, soit ceux qui proviennent de l'ensemble du lac (p. ex. les changements du niveau et de la chimie de l'eau, l'introduction d'espèces exotiques) et ceux qui proviennent des terres adjacentes (p. ex. la contamination due à des sources ponctuelles et la sédimentation). Il n'est pas possible de limiter à l'échelle locale les stress dus à l'ensemble du lac mais, par contre, ceux qui proviennent d'activités terrestres sont plus faciles à gérer. Les changements lents auront vraisemblablement des effets moins marqués que les changements rapides, mais un petit changement peut avoir des effets catastrophiques s'il dépasse le seuil de tolérance d'un Ècosystème. On peut également noter de fortes altérations de tout un écosystème si une espèce unique, mais importante (p. ex., un macrophyte) est perturbée, à cause de rétroactions complexes entre les différents éléments du système. Par conséquent, les stratégies de gestion doivent porter plus spécialement sur les zones qui sont particulièrement sensibles aux stress provenant des terres voisines et à ceux qui ont le plus de chances de dépasser le seuil de tolérance de composants clés d'un écosystème.
[Traduit par la Rédaction]

Introduction

The aim of this paper is to focus the attention of managers who are responsible for conservation or enhancement of coastal habitats on *(i)* the mutability of these habitats and *(ii)* rates of change of ecosystem processes in them. The types of managerial actions likely to be undertaken, including structural, chemical, or biotic alterations, are discussed by Geiling et al. (1996) in this issue. If a habitat is changing rapidly, should resources be used for its conservation or enhancement? Are coastal habitats, to use the terms of this workshop's introduction, "constant and continuing?" Can stresses likely to prevent conservation be detected in these areas?

The region selected for discussion is the Kingston Basin of Lake Ontario (Fig. 1). It includes the lake shore and the estuarine portions of the rivers entering the Basin. The boundary between aquatic and terrestrial ecosystems is well defined along most of the shore, but is often diffuse in wetlands; cottage lots and marshes, for example, form a vegetational continuum in some parts of the basin (McLaughlin 1993). Before examining changes, the present types of shoreline in the Kingston Basin are described and their geological age is briefly discussed.

The term "habitat" is used to define both the area used by a particular species, such as "pike habitat," and a type of environment, such as a "cattail marsh" or a "sandy bay." The first usage can cause difficulties because of the overlapping use of an area by different groups and species of organisms. Some species remain in a particular habitat all their lives, while others move through wide geographic areas and use several

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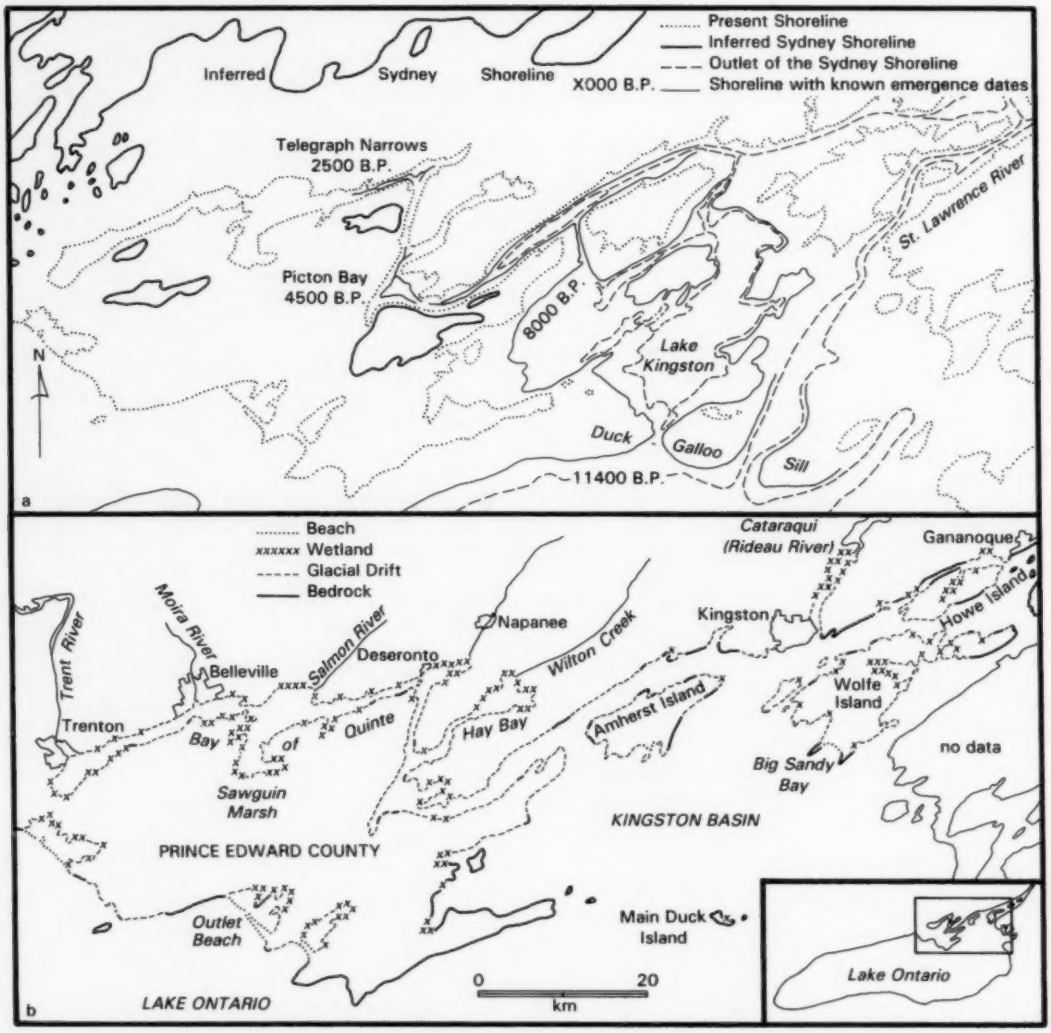
Fig. 1. *(a)* Development of the Kingston Basin, with the present shoreline shown by a dotted line. The Sydney shoreline in the north preceded the 11 400 yr BP phase, which had an outlet indicated by a broken line. Where dates are known for younger portions of the shore these are shown. *(b)* The distribution of beach, wetland, glacial drift (till), and bedrock on the shores of the Kingston Basin, which is also shown in the inset.



types of site. In this volume, Geiling et al. (1996) develop a model of fish habitat based on three components, physical, chemical, and biotic, which vary through space and time. We use examples of these three components to examine temporal changes in coastal habitats in the Kingston Basin. To discuss changes in physical components we have selected water levels and sedimentation (sections A and B). For the chemical component we have selected acidity, salinity, nutrient status, and contamination (sections C, D, E, and F). To discuss changes in the biotic component we have selected communities of algae, macrophytes, fish, reptiles and amphibians, and piscivorous birds (sections G, H, I, J, and K). Rates of introduction of exotic species are discussed in Section L. Where possible, interactions between the three types of component are emphasized.

A change in any of thse components will impose a stress on an ecosystem. Depending on the magnitude and rate of change, the ecosystem responds to that stress in one of five ways (Keith 1994): *(i)* the ecosystem continues to function but with "hiccups"; *(ii)* it continues to function but at a lower level, for example, of diversity or productivity; *(iii)* it incorporates new features, such as exotic species; (*iv*) it functions, but differently; or (*v*) it collapses without regeneration.

Which of these ecosystem changes are apparent in modern and past habitats in the Kingston Basin? Do the coastal wetlands or the nearshore zone exhibit cycles of aging and enju-

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venation, which have been postulated for some fish communities (Sly 1991)? Do they exhibit slow and steady changes, or do they reach threshold values followed by catastrophic events (Minns et al. 1986)? While these questions have previously been considered in the context of Lake Ontario as a whole (Christie 1973; Sly 1991; Stoermer 1993), attention has not previously been focussed on changes in nearshore habitats.

Description of shoreline habitats in the Kingston Basin

The lengths of different types of shoreline were abstracted from the Coastal Zone Atlas (for types cf. Cowardin et al. 1979; Geis 1985). The largest component (by length of shoreline) is glacial drift or till (57%), followed by bedrock (21%), wetlands (15%), and beaches (5%). The balance (2%) includes docks, marinas, etc. Comment on these types of shoreline follows, giving some named examples and references. Locations are shown in Fig. 1.

Bedrock is Palaeozoic limestone in the west and mostly Precambrian Shield rocks east of Kingston. The rock areas include large cliffs, which are excluded from discussion here (e.g. Main Duck Island, middle Bay of Quinte). Examples of gently sloping bedrock shores include parts of the Bay of Quinte (Crowder and Bristow 1986; Dushenko 1990; McLaughlin 1993), Collins Bay (Browne 1991), Deadman Bay (east of Kingston), Amherst Island and Wolfe Island (Johnston 1972, 1978), and the St. Lawrence River (Ruta 1981).

A veneer of glacial till or glaciolacustrine silt and clay covers much of the bedrock and forms steep shores in areas protected from erosion such as parts of Cataraqui Bay. Elsewhere, this sediment has been eroded and fringing beaches of sand and gravel formed from the winnowed, coarser fraction protect the remaining glacial sediments behind. Only at the highest water level do the glacial sediments come in contact with the lake.

Beach habitats generally are exposed to a long fetch facing the southwest prevailing wind, and include Presqu'ile and Outlet beaches in Prince Edward County and Big Sandy Bay on Wolfe Island (Law and McKenna Neuman 1993). These beaches are favourite staging areas for migratory waterfowl (references in Crowder and Bristow 1988).

Wetlands comprise three main types: lagoons behind barrier beaches, embayed wetlands, and riverine estuaries. Wetlands behind barrier beaches occur in the same situations as beaches, e.g., on the west side of Prince Edward County and Wolfe Island, where the barriers are sand, and in sites such as Yorkshire Island on the Main Duck Sill and Prince Edward Point, where the barriers are gravel or cobbles. Barriers may be breached by storms or high water levels, allowing lake water into lagoons. The most fragile wetlands in the area are probably intradune pannes, which are habitat for some rare plants in the Prince Edward County sand dunes (Law and McKenna Neuman 1993).

Embayed wetlands occur where the form of the shore offers protection from wind and wave action. Numerous small embayed wetlands sheltered from the prevailing southwest winds have been described by Greig (1989), Dushenko (1990), and McLaughlin (1993) in the Bay of Quinte. Embayed wetlands on Wolfe Island were described by Price (1994). Embayed wetlands are affected primarily by stresses of lake origin because of the absence of significant river influence (cf. Dalrymple et al. 1992).

Riverine wetlands occur in the lower reaches of large rivers or small creeks in the region. The Cataraqui River exemplifies their freshwater estuarine form, influenced both by river flow and lake action (Dalrymple and Carey 1990; Dalrymple and Price 1994). The estuarine nature of the river marshes is emphasized by occasional seiche-induced bores in the lower Napanee River. Sediments in the marshes include peat, gyttja, clay, and sand (Fig. 2). Following Dalrymple et al. (1992), we emphasize that estuarine wetlands are impacted by stresses derived both from Lake Ontario and from the adjacent land area.

The large river mouths have been drastically altered in the last 200 years. Dams were built on most rivers, including the Trent, Moira, Salmon, Wilton, Napanee, Cataraqui, and Gananoque systems. The mouth of the Salmon system was quarried for aggregates, creating new lagoon areas. Flow has been restricted by roads and railway embankments (e.g., in Landon Bay and in creeks from Belleville to Deseronto) and dams made for duck habitat (Mud Creek). Urbanization has "hardened" the lower banks of the major rivers, and in most cases their flow is controlled. The most valuable fish habitat now occurs in the least developed areas including Hay Bay (Wilton Creek) and Muscote Bay. Despite urbanization, however, the lower Trent River is still a walleye breeding habitat (Bay of Quinte RAP Committee 1990).

Vegetation in the wetlands includes submerged, floating, and emergent marsh types; woody shrub thickets; and swamp forests. The most widely distributed wetland vegetation type in the Kingston Basin (as distinguished from the geomorphic types described above) is cattail marsh (Crowder et al. 1977; Revill Associates 1979; Catling 1985; Crowder and Bristow 1986).

How old is the present shoreline?

The Kingston Basin was part of glacial Lake Iroquois, which formed when retreating Laurentian ice dammed the St. Lawrence valley about 12 400 yr BP. Under harsh cold conditions, thick deposits of glaciolacustrine sediments (mainly clays in the study area) were deposited over bedrock and glacial till. The present landscape was then gradually revealed as water levels fell during the next 1000 yr (Anderson and Lewis 1985; Naldrett 1991; Gilbert and Shaw 1992; Gilbert 1993).

By 11 400 yr BP (Fig. 1), the St. Lawrence valley was open. Isostatic depression to the northeast lowered the Lake Ontario outlet, then situated south of a sill at Greater Main Duck and Galloo Islands, to a level about 40 m below the present level, allowing incursion of the Champlain Sea to the Ontario Basin (Andrews 1970; Anderson and Lewis 1985; Fulton and Richard 1987; Gilbert 1993). All of the study area was exposed at this time. In the Kingston Basin, small lakes formed in depressions and a river system drained to the east on the newly exposed lake floor. Evidence of large wetlands along this river and lake system, similar to those of the present Cataraqui River, has been found at an elevation 15–20 m below the present-day Lake Ontario surface (Gilbert and Shaw 1992). Subsequent isostatic rebound and uplift of the St. Lawrence River caused lake levels to rise, flooding the coastal area again. The isolated lakes in the Kingston Basin

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Fig. 2. *(a)* Stratigraphy and chronology of sediments on a north–south transect of the lagoon of the Cataraqui River, Kingston, Ont. Glaciolacustrine clay is overlain by marsh sediments, including gyttja and peat. Asterisks show depths at which samples analyzed for radiocarbon dating were collected. *(b)* Deposition of peats and gyttja in relation to lake levels, with two peat surfaces that were flooded. *(c)* Relationship between water levels and sediment surfaces during the last 4000 yr (from Dalrymple and Carey 1990).

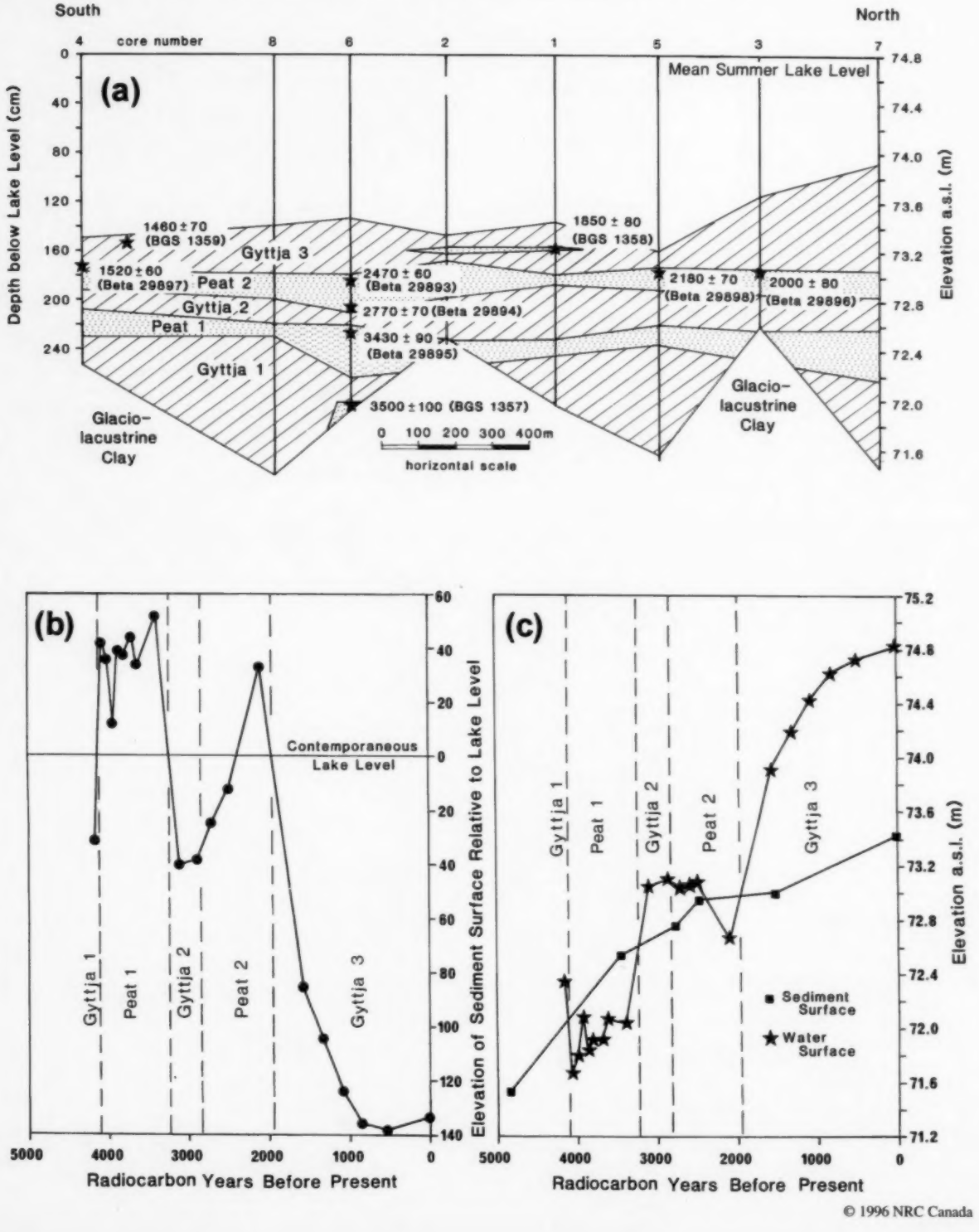

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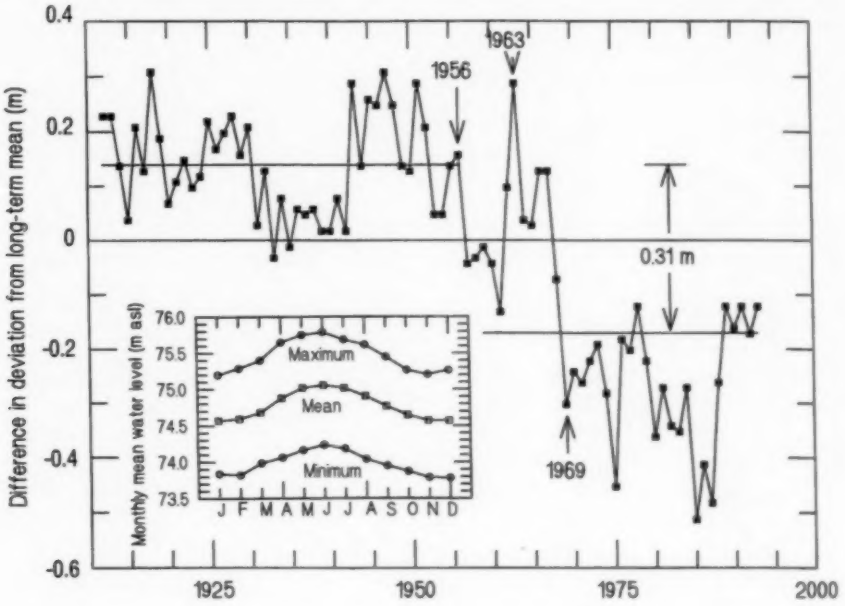
Fig. 3. Annual differences from the long-term mean water level of the Kingston Basin since 1910: the St. Lawrence Seaway opened in 1957. The inset diagram shows the annual pattern of maximum, mean, and minimum monthly water levels. Levels are in metres above sea level.



gradually enlarged and merged with Lake Ontario, probably before 8000 yr BP (Gilbert and Shaw 1992). Water levels reached present or somewhat higher levels (within 2–3 m) by about 4000 yr BP. The last parts of the basin to be flooded were in the Bay of Quinte: Picton Bay was flooded by 6000 yr BP; while Sly (1986) indicates that the northern part of the bay, west of Telegraph Narrows, was not part of the main lake until after 2500 yr BP.

The age of present shore habitats therefore varies, with few exceeding 2000 yr, in comparison with the 10 000 yr history of some inland basins in the drainage area of the rivers entering the Kingston Basin (Terasmae 1968).

Temporal changes in habitat components in the Kingston Basin

Physical components

(A) Water levels

Isostatic tilting is still occurring in Lake Ontario. The eastern outlet of Lake Ontario is rising with respect to the western end at a rate of about 1.8 mm·yr^{-1} (Clark and Persoage 1970; Sly and Prior 1984; Anderson and Lewis 1985). This movement is sufficiently slow for wetlands and their plants to remain in equilibrium with it. Superimposed on this long-term change are shorter term events including the following:

(1) seiches and storms, with an amplitude of centimetres or decimetres, lasting a few days (Dalrymple and Price 1993);

(2) seasonal changes (Fig. 3) generally varying by about 0.5 m in 6 months (Price 1994);

(3) interannual and decadal differences of up to 1 m, resulting from the changing balance of precipitation and evapotranspiration (Bishop 1987) (Fig. 3); and

(4) long-term oscillations of 0.5–1 m with periods of the order of 200–300 yr, presumably due to climate changes (Dalrymple and Carey 1990).

Fractal analysis of the historical record of mean annual water levels in Lake Ontario (Fig. 3) indicates that water levels vary continuously at all temporal scales, so that it is inappropriate to speak of discrete periods or cycles. Lake Ontario wetlands are described as "pulse stabilized" rather than cyclic (cf. IJC Functional Group 2 1989; Planck 1993; Wilcox 1993).

Important questions for managers are whether global warming is occurring (Pocklington 1994) and, if so, what effects it could have on water levels in the Great Lakes region. Current models vary in assessing the balance between precipitation and evaporation, with resulting predictions ranging from a drop of 1.5 m to a rise of the same magnitude (Rogers and Harshadeep 1994).

The effects of level changes that have occurred in the past are exemplified by observations in the estuarine part of the Cataraqui River (Fig. 2). Two periods of flooding followed by lower water levels are shown in the sediment record, with high water coinciding with warm periods (Dalrymple and Carey 1990; Dalrymple and Price 1994). The marsh responded to this stress in two ways: *(i)* sediment and vegetation changed gradually over most of the period, but *(ii)* two sharp thresholds occurred when a peat mat was flooded. At these thresholds the wetland appears to have changed abruptly from an emergent marsh, accumulating peat, to an open-water lagoon with submerged plants, accumulating gyttja. Thus, the ecosystem continued to function, but differently, showing the type of response to stress in the fourth category distinguished by Keith

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(1994). These events in the sedimentary history are probably similar to modern flooding events described by Jaworski et al. (1979) and Quinlan and Mulamoottil (1987).

Is the present water-level regime of this region affected by the St. Lawrence Seaway? Water levels for the years 1912–1993 were compared for Lakes Ontario and Erie, and it was evident that Lake Ontario is subject to larger changes of level than Lake Erie and that the curves for the two lakes diverged in the late 1960s. Annual differences from the long-term mean for Lake Ontario (Fig. 3) indicate that the lake was lower than normal at the time of the St. Lawrence Seaway opening in 1957. Comparing the periods 1912–1956 and 1969–1993, we found a lowering from the predicted mean in the later period. Since 1968, Lake Ontario has been consistently lower than its long-term mean by about 0.3 m. Therefore, the Seaway can be expected to have caused habitat changes, allowing woody growth, cattail marshes, and submerged plant beds to shift downslope.

The current regulation plan of Lake Ontario is designed to keep lake levels within a range of 1.2 m; in reality they vary with a range of approximately 2 m (IJC Levels Reference Study Board 1993).

(B) Sedimentation

Changes in rates or types of sedimentation are important in nearshore habitats because different fish communities are associated with different sediment types, and because turbidity and rapid sedimentation can damage some organisms. The associations of fish with different sediment types such as wood debris, gyttja, sand, etc. have been described by Keast et al. (1978), Keast (1984), Stephenson (1990), Jude and Pappas (1992), and Eadie and Keast (1994). If as cores from the Cataraqui River (Fig. 2), Deadman Bay, and other sites show (Johnston 1972; Dalrymple and Carey 1990) local habitats have undergone sudden alterations of sediment type in the past, their associated fish communities are likely to have changed too. As an example of such change, rapid sedimentation of dead *Cladophora* and *Myriophyllum* was reported to prevent lake trout (*Salvelinus namaycush*) from spawning successfully, by covering some spawning beds in the Kingston Basin during the 1960s (Sly 1991).

Events such as storms can significantly change the rate of sedimentation. Lacking evidence from the study area, a well-documented case can be cited from New York State when a 1972 hurricane caused 17 cm of rain to fall in 24 h. In Lake Canandaigua, light transparency decreased rapidly (Secchi disc readings fell from 3.5 to 0.5 m in 12 h) because of riverine input, returning to prestorm values in about a month. In Lake Canandaigua the algal community changed, and in Lake Cayuga the macrophyte community lost biomass and became dominated by *Myriophyllum* (Oglesby and Vogel 1976; Eaton and Kardos 1978). Presumably, storm events and subsequent changes in sediment loads can similarly affect the nearshore of Lake Ontario.

Sediments along the shoreline of the Bay of Quinte show high spatial patchiness (Dushenko 1990). Samples from 0.5–m water depth all contained some fine sand and some organic content; in addition, 79% had coarse sand, 77% silt, 39% gravel, and 20% clay. In cattail marshes, substrate patchiness is also high, with the organic content ranging from 38 to 76% (Greig 1989). Such patchiness also occurs in older sediments; in 12 cores collected within Deadman Bay (Johnston 1972) the number of layers with shells ranged from 0 to 10 and the number of layers with wood fragments ranged from 0 to 3. These data illustrate the heterolithic nature of shallow water environments, creating habitat changes for their biota as sedimentation regimes alter.

From the managerial point of view the effects of development on sediment type are notable. Johnston (1972) in Deadman Bay, Frape (1979) in the Cataraqui River, and McLaughlin (1993) in the Bay of Quinte have all noted differences in sediment type associated with runoff from developments. These include cottages, condominiums, industrial plants, and marinas.

Marl, an unconsolidated sediment composed of calcium carbonate (calcite), occurs in layers in postglacial organic sediments from lakes, wetlands, and stream valleys, inland from the Lake Ontario shore between Belleville and Kingston (Guillet 1969; Vreeken 1981, 1994). Long-term rates of marl accumulation inland have ranged from 0.03 to 0.47 $cm \cdot yr^{-1}$. Lake "whiting' events (visible precipitation of marl) are now being observed in Lake Ontario on an increasingly frequent and large scale. In the last 50 yr, calcite in sediments in the Niagara basin has increased by an order of magnitude, and in the Rochester Basin, calcite precipitation began about 1920 (Schelske et al. 1988). In the Kingston Basin, calcium carbonate was precipitated near Wolfe Island in at least 5 of the 7 yr between 1977 and 1983 (Sylvestre et al. 1987). The cause is generally considered to be uptake of CO_2 by algae, causing pH to rise, so that the epilimnion becomes supersaturated with calcium and carbonate resulting in precipitation. Marl in a core from the Bateau Channel is considered to be similar in origin (Gilbert 1990).

Impacts of whitings on organisms in the nearshore zone are not known. Marl deposits on macrophytes in the study area vary within the summer and between years (Crowder et al. 1977; Crowder and Bristow 1986), presumably because water temperatures fluctuate (Gilbert and Leask 1981). Marl deposition increases during eutrophication and has been suggested as a factor causing declines of macrophytes (De Nie 1987).

Chemical components

(C) Acidity

Discussions of increasing acidity due to acid precipitation have generally excluded Lake Ontario because it is well buffered (Charles 1991). In surface sediments in the Bay of Quinte, however, the pH ranges from 9.3 to 5.5 (Dushenko 1990) and in Quinte cattail marshes water pH ranges from 7.6 to 5.5 (A.A. Crowder, unpublished data). Acid precipitation or drainage has maximal effect in marshes with limited lake influence. Potential for acid shock in spring runoff was discussed by Sly (1991). Because niches of many coastal and wetland organisms are sharply defined by their pH tolerance, further acidification of marsh or shoreline habitats could result in community changes. Amphibian eggs, for example, are sensitive to increased acidity (Scheuhammer 1991). The rate at which acidity causes community change can be rapid; for example, algal communities can change within a season (Charles 1991).

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(D) Salinity

Sodium chloride is an example of an inorganic industrial compound added to the Great Lakes in the last two centuries. Until about 1910, salt concentrations in Lake Ontario were steady at approximately 8 ppm. They then began to increase by approximately 4% per decade, with the rate slowing to 3% per decade in the last 30 yr (Beeton 1965; Johnston 1972; Pringle et al. 1981; Sly 1991). Creeks in the Kingston Basin show high concentrations of chloride in spring; road salt is considered to be the source (Ralston and Hamilton 1978; Crowder and McLaughlin 1993a; Stride 1993).

Salt-tolerant species are among the exotics that have invaded Lake Ontario (Mills et al. 1993). They include algae, invertebrates, fish, and macrophytes. The macrophyte community in the Bay of Quinte has become less diverse in the last half century; when the growth of common plant species from the Bay was tested in a range of salt solutions, the most halophilic species was *Myriophyllum spicatum*, which dominated the Bay during its most eutrophic period (Crowder and Bristow 1986; McLaughlin 1993). The present dominant, *Vallisneria americana*, is also salt-tolerant (Korschgen and Green 1987).

(E) Nutrient status

Eutrophication has been documented in the Kingston Basin most thoroughly for the Bay of Quinte (Minns et al. 1986; Bay of Quinte RAP Committee 1990). Historic episodes of enrichment by phosphorus are recorded by sediment and fossil changes in the Bay, and a major enrichment phase began in the 1930s, culminating in hypereutrophication and followed by control of point-source phosphorus inputs after 1978. Because of control, offshore P concentration during the ice-free season has now been lowered to a mean of 37 $\mu g \cdot L^{-1}$ (Bay Of Quinte RAP Committee 1990).

Nearshore sites have not necessarily followed the lakewide pattern of a decrease in eutrophication since the 1970s, if they are affected by local sewage inputs or land drainage. Examples of local areas currently experiencing eutrophication include the lower Napanee River, Hay Bay, Landon Bay, Collin's Bay, and the Little Cataraqui River (Bay of Quinte RAP Committee 1990; Browne 1991).

(F) Contamination

Loading of metals and organic compounds in Lake Ontario has recently been reviewed by Allan and Ball (1990). Loading of both increased until the early 1970s and has since been decreasing. This trend is shown by data from the Moira River (Fig. 4) for metals and phenolics.

In the nearshore, local sources of contamination are important. Metals have been derived from local industries, largely situated on the main river valleys; from waste dumps; and from mining and smelting. Mining began in the Moira Valley in the mid-19th century and has left a legacy of tailings, which are now treated to precipitate arsenic (Johnston 1978; Mudroch and Capobianco 1980; Paehlke et al. 1982; Crowder 1994). To prevent contamination of the Moira River this treatment will have to continue indefinitely. In 1990 the influence of the mines was still apparent in elevated concentrations of Cr, Cu, Ni, and Co in shoreline sediments, attenuating with distance away from the mouth of the Moira River (Dushenko 1990). Metals currently exceeding provincial guidelines for aquatic life in the Bay of Quinte include Cr, Hg, Mn, Fe, Cu, Pb, Zn, and the metalloid As (Poulton 1992).

Organic compounds, which peaked in loading during the 1970s, included herbicides and pesticides. Substances causing concern in the Kingston Basin at present include phenols and pentachlorophenol (Bay of Quinte RAP Committee 1990). Substances commonly reported in local analyses include trichlorobenzenes and hexachlorobutadiene, hexachlorobenzene, DDE, and DDT (Poulton 1992).

Habitats contaminated by organics include river mouths and wetlands near waste dumps; that is, sites with local terrestrial inputs. Examples include the Trent and Cataraqui rivers and Picton Marsh Creek. Some nearshore sites have sediments contaminated by both metals and organic compounds (Johnston 1978; Frape 1979; Creasy 1981; Minns et al. 1986; Bay of Quinte RAP Committee 1990).

Biotic components

(G) Algae

Changes in the algal community of Lake Ontario have been shown by microfossils, mainly diatoms and chrysophytes, extracted from sediment cores (Schelske et al. 1988; Schelske 1991; Stoermer 1993). Deductions about historic or prehistoric lake conditions can be made by statistical comparisons of dated microfossil assemblages with algal assemblages from present-day lakes; "calibration sets" of present-day lakes for such comparisons have been selected to show gradients of water chemistry and physical conditions. Such gradients include acidity, salinity, P content, and temperature, because the specific niches of algae are differentiated by such factors (Charles 1991).

In Lake Ontario, algal assemblages have shown little stability since the 18th century. Since 1770, at least 11 separate algal zones can be distinguished, using cluster analysis of the most abundant diatom taxa (Stoermer et al. 1985). Five phases are generally recognized in the diatom assemblages:

(1) a fairly steady state prior to 1770, with P as the limiting element;

(2) increased diatom accumulation with increased anthropogenic nutrient loading;

(3) decreased diatom accumulation, with silica the limiting element during summer stratification;

(4) further decrease with silica limitation during periods of lake circulation; and

(5) increased diatom accumulation with reductions in phosphorus loading since the 1970s.

Diatom assemblages in the lake can show rapid changes. Sly (1991) pointed out that in the Bay of Quinte an oligotrophic assemblage in 1835 had changed to a eutrophic one by 1852; during that period lumbering, farming, and industry were rapidly changing water chemistry, amount and temperature of runoff, turbidity, and rates of sedimentation (Warwick 1980; Sly 1991). The group of algae considered most sensitive to such changes are not diatoms, but chrysophytes; Lake Ontario sediments show a rapid decline in chrysophyte numbers during the period 1831–1847 (Stoermer 1993). The declines of diatoms and chrysophytes have not been indicative of overall lowered algal productivity as eutrophic conditions have gen-

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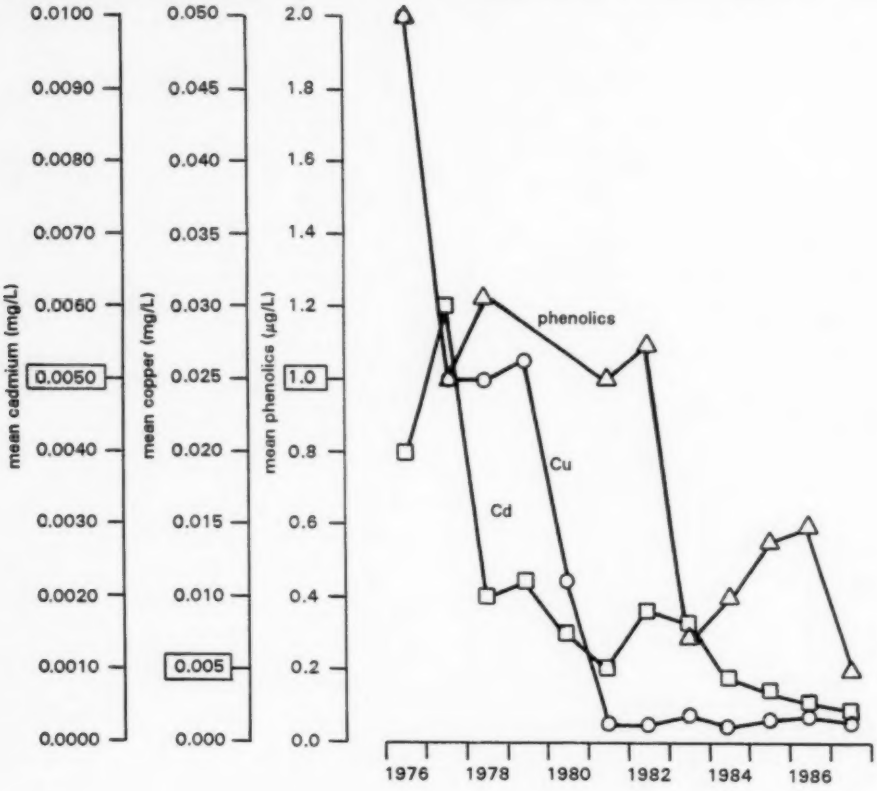
Fig. 4. Mean annual concentrations of cadmium, copper, and phenolic compounds in the lower Moira River from 1976 to 1988. Boxes indicate the Ontario water quality objectives for protection of aquatic life. Data are from Beak Consultants (1988).



erally allowed increases in biomass and productivity of blue-green and filamentous green algae (Bay of Quinte RAP Committee 1990; Minns et al. 1986).

The general trends in algal communities of Lake Ontario described above have been based on samples taken from open water areas; trends in nearshore or wetland algal communities can be different, because inshore nutrient supplies may be increased by pulses of riverine loading (Stoermer 1993). An example of opposite trends in the open lake and an inshore site is provided by algae in Hamilton Harbour – Coote's Paradise (Yang et al. 1993) since the 1970s. While diatom numbers in open water have been increasing during this period, diatoms have decreased in numbers and diversity in this inshore habitat. The number of diatom species before the year 1800 was 28–37, which increased to a maximum of 55 about 1900, and declined to 23 by 1986. Rapid change after 1970 has been attributed to turbidity, eutrophication, and contamination (Yang et al. 1993).

The Kingston Basin has not lost species in this drastic way. Following extreme eutrophication and point-source P control in the Bay of Quinte about 300 phytoplankton species now occur, with diatoms predominating in early summer, followed in late summer by blue-greens. Control of point-source P has decreased offshore algal biomass but has not altered the dominant species.

Inshore, *Cladophora* blooms were abundant in the Kingston Basin, and in the Bay of Quinte during the 1960s and 1970s before control of point-source P, but these subsequently declined (Painter and Kamaitis 1985). Quantitative data are not available on current inshore algal communities in the Kingston Basin, although algal blooms are frequently observed in bays and marshes (Browne 1991; McLaughlin 1993).

For a manager of fish habitat the importance of frequent or major changes in algal communities, such as those described above, lies in structural impacts (e.g., those due to *Cladophora*), in changes in light penetration affecting submerged plant growth and fish behaviour (e.g., during blue-green blooms), and in changes in availability of specific food items for invertebrates.

(H) Macrophytes

Eutrophication first causes increases in biomass of algae and macrophytes, causing fouling of fish nets and propellers. A scenario follows, described for many sites in Europe and the eastern seaboard of the United States (De Nie 1987; Carter and Rybicki 1985, 1986), in which the macrophytes decrease in biomass and become confined to shallow areas. The decline is due primarily to shading, as turbidity increases because of plankton, dead material, and inorganic particles. The change

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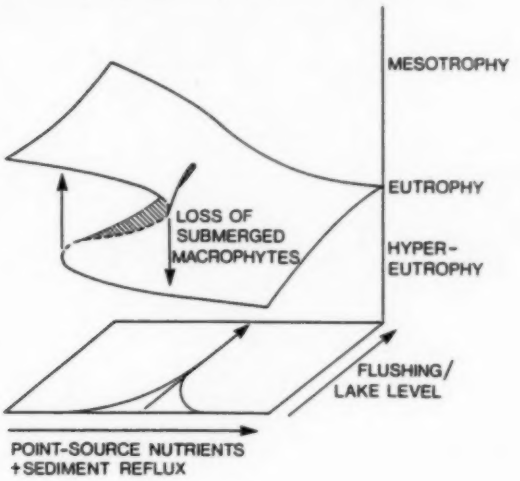
Fig. 5. A catastrophe model for change in submerged habitats in the Bay of Quinte (after Minns et al. 1986). Point-source nutrients and sediment reflux caused an increase in the density of algae, which resulted in shading of submerged macrophytes. At this hypereutrophic state, macrophyte beds died off rapidly. Suspended sediment has slowed recovery of the macrophytes although point-source phosphorus loads have been decreased.



in area of macrophyte beds can occur rapidly; for example, they may shrink by 25% of their area per year as deeper sites become turbid (De Nie 1987). A predictive equation for turbidity (measured as Secchi disc depth) was developed from data from Organization for Economic Co-operation and Development lakes, showing that increased loading of dissolved phosphorus results in increased concentration of chlorophyll *a*; the greater algal density decreases light penetration, causing Secchi disc readings to decrease (Vollenweider and Kerekes 1982).

In the Kingston Basin, there is anecdotal evidence of an increase in biomass of macrophytes during the 1960s, in the Bay of Quinte, coinciding with an increase in *Cladophora* (Crowder and Bristow 1986; Painter and Kamaitis 1985). During the 1970s the area of macrophyte beds and the biomass of macrophytes were extremely low (Crowder and Bristow 1986), coinciding with Secchi disc measurements less than 1.5 m.

Decline in area, biomass, and species richness of macrophytes in the Bay of Quinte during eutrophication was fitted to a catastrophe model (Minns et al. 1986). Once the decline of macrophytes had reached a critical value the ecosystem changed, functioning at a lower level (Fig. 5). Loss of fish habitat was part of the temporal change. Recently, some other areas in the Kingston Basin have had high turbidity and low biomass of submerged macrophytes because of local eutrophication (Browne 1991).

After P loading has been limited, greater water clarity and increased submerged macrophyte biomass and area have been reported in numerous European lakes (Sas 1989). Control of point-source P in the Bay of Quinte since 1978 has resulted in decreased algal biomass and a 0.2-m increase in mean Secchi disc measurements in open water (Bay of Quinte RAP Committee 1990). Inshore zones responded more slowly; light penetration had not increased by 1990, mainly because of the presence of seston in early summer and plankton in late summer (Dushenko 1990). By 1993, however, with improved light penetration, submerged macrophyte beds had increased in area and in biomass (Crowder and McLaughlin 1993*b*). The first colonists in deep areas were frequently charophytes (Revill Associates 1988; Dushenko et al. 1990; Crowder and McLaughlin 1993*b*). Light conditions appear to be changing rapidly in the mid-1990s because of zebra mussels (*Dreissena polymorpha*) (see Section L).

Introduced carp (*Cyprinus carpio*) ingest macrophytes and stir up sediment (De Nie 1987; Painter et al. 1988). Resuspension of sediment particles by carp is considered largely responsible for absence of submerged macrophytes in Hamilton Harbour – Coote's Paradise in western Lake Ontario (Painter et al. 1988). After experimental removal of carp, macrophytes can recolonize an area within weeks if propagules are present (Netherlands Ministry of Transport 1989). Carp are abundant in the Kingston Basin (O'Dacre 1992) and are known to ingest macrophytes in the Bay of Quinte (Powles et al. 1983). They could affect the structure of habitats, particularly in sheltered lagoons.

The areas of some emergent marshes in the basin have increased, but only descriptive data record this increase (Crowder and Bristow 1986). The drop in water levels since the construction of the St. Lawrence Seaway (a long-term drop of approximately 0.3 m in mean level, see Section B) should have allowed emergent marsh plants to move offshore and woody zones to shift downslope slightly (cf. Fig. 3). Although the long-term mean has been changed, fluctuations about the mean are sufficient to prevent marsh zones becoming static.

(I) Fish

Marked changes in the fish community of Lake Ontario have occurred in the last century (Christie 1973; Hurley 1986; Sly 1991). If harvest quantities can be assumed to reflect relative abundance of species, some of these changes, such as decreased abundance of lake whitefish (*Coregonus clupeaformis*) and lake trout, are shown in Fig. 6. Changes in the population size of less abundant species, such as lake sturgeon (*Acipenser fulvescens*), are not shown.

Four possible causes of these changes are listed below.

(1) Changes of water temperature regimes. Deforestation is likely to have increased the temperature of stream waters in the region, beginning in the 1830s (Sly 1991). Warming trends may have diminished salmon spawning success, caused die-off of alewife (*Alosa pseudoharengus*), and increased spawning success of sea lamprey (*Petromyzon marinus*) (Sly 1991). In other periods, unusually cold winters are considered responsible for declines of warmwater fish such as white perch (*Morone americana*) (Christie 1973). Degraded coastal habitats, such as those affected by urbanization, are considered to favour warmwater species including white perch, common carp, suckers, and gizzard shad (*Dorosoma cepedianum*) (Holmes 1988). The present fish community of coastal waters has been described by Stephenson (1990) and by Jude and Pappas (1992) and contains several warmwater species.

(2) Introductions of exotic species, including carp (about

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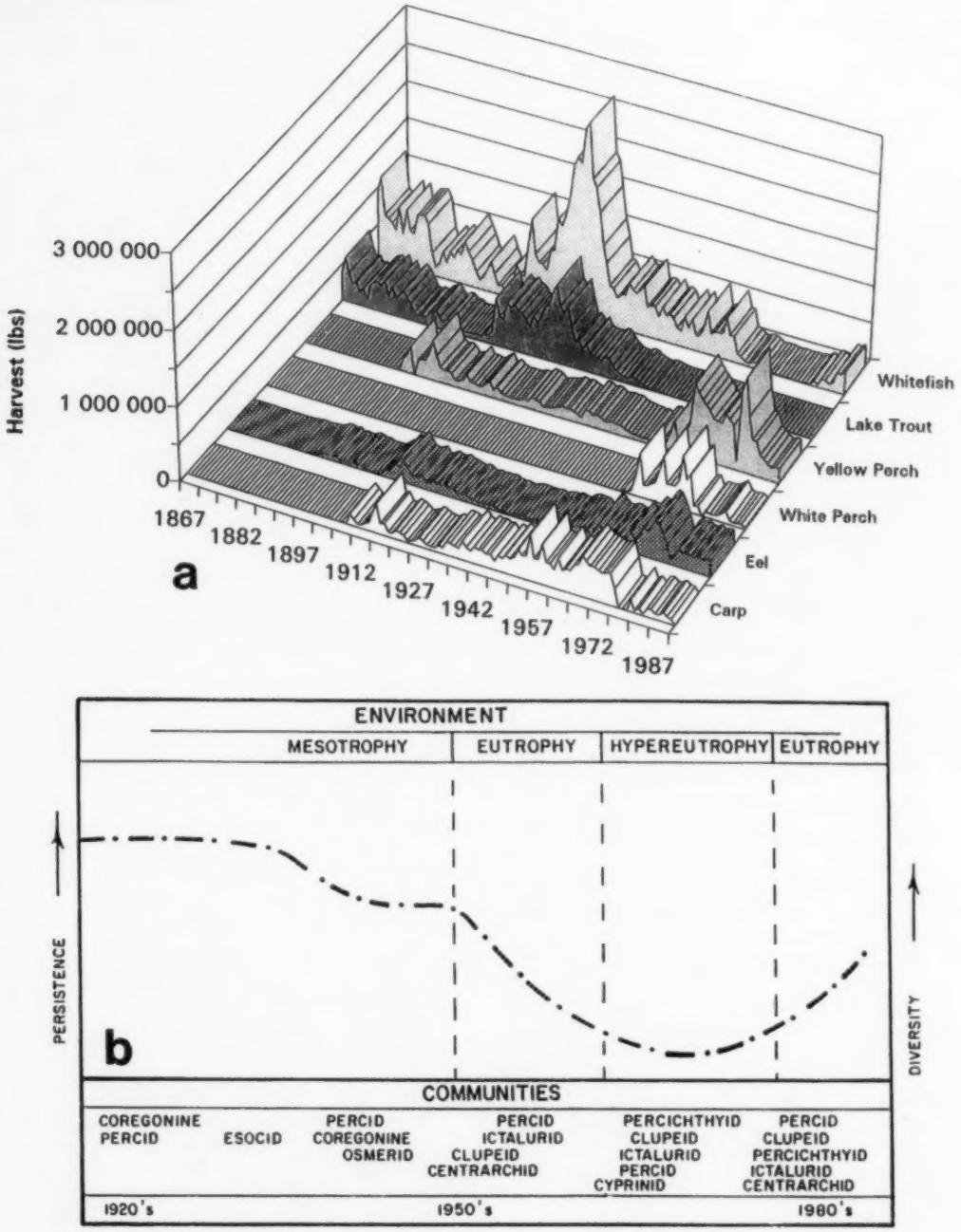
Fig. 6. (*a*) Rapid changes in populations of six species of fish in Lake Ontario from 1867 to 1987, as shown by commercial harvests (in lbs.). Data from Ontario Ministry of Natural Resources, Napanee, Ont. (*b*) Changes in the fish community of the Kingston Basin during the period 1920–1990, showing a loss of dominance by coregonid fish. Diversity was lowest during the late 1960s (after Sly 1991). The temporal scale is that of Sly (1991).



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1879), resulting in loss of macrophyte habitat (Jude and Pappas 1992).

(3) Changes in water chemistry, including decreased oxygen in bottom waters during decay of dead algae and macrophytes during eutrophication. This has the effect of making bottom waters unusable by species such as lake trout.

(4) Overfishing of piscivores, resulting in unbalanced and rapidly changing food webs (Minns et al. 1986, 1987).

The fish community of the Kingston Basin shows some of the responses to stress listed in the introduction. New features have been incorporated in the ecosystem, such as stocked salmonids, and the ecosystem functions differently from the way it did a century ago, with its main economic value now derived from walleye (*Stizostedion vitreum*). About 20 species of fish use shoreline habitats in Lake Ontario (Stephenson 1990; Jude and Pappas 1992) and their populations can be regarded as being unstable and unpredictable in occurrence.

(J) Amphibians and reptiles

Wetlands and coastal waters in the Kingston Basin are year-round habitats for snapping (*Chelydra serpentina*) and painted turtles (*Chrysemys picta*), salamanders, bullfrogs (*Rana catesbiana*), and green frogs (*Rana clamitans*). Anecdotal evidence of declining abundance of these taxa is widespread (Cook 1989; Bay of Quinte RAP Committee 1990; OMNR 1994*b*). Some of their early developmental stages, including eggs, are sensitive to metals such as aluminum and copper, especially under acid conditions (Freda 1991). A decrease in abundance of snapping turtles in the study region has been attributed to organic contaminants in their eggs; eggs of snapping turtles collected from the Bay of Quinte contained PCB, dioxin, furans, and dieldrin and showed a high proportion of dead or deformed embryos in comparison with uncontaminated eggs collected from a control site in Algonquin Park (Struger et al. 1993). In addition to food-chain effects, turtles alter habitat by grazing.

(K) Piscivorous birds

Colonies of some fish-eating birds in Lake Ontario, including common terns (*Sterna hirundo*), herring gulls (*Larus argentatus*), and double-crested cormorants (*Phalacrocorax auritus*), had decreasing numbers of birds in the 1960s. Reproductive failures were found to be caused by thin eggshells that were easily broken, embryos that died during incubation, and unusual incubation behaviour by adult birds (Swain 1981). A high proportion of chicks with deformities was also observed, including common terns with crossed bills, small eyes, and two pairs of feet (Gilbertson et al. 1989). Sites in the Kingston Basin where reproductive failures were monitored and where deaths and deformities were found to be correlated with organic contaminants in eggs of gulls and terns included Snake Island, Pigeon Island, and Little Galloo Island (Struger et al. 1987; Fox and Weseloh 1987; Weseloh et al. 1989; Gilbertson et al. 1989).

Since the late 1970s concentrations of contaminants in the birds' eggs have decreased, although not steadily (Gilbertson et al. 1989). In the eggs of herring gulls from Snake Island, dioxin (2,3,7,8,-TCDD) concentration fell from 175 ppt in 1981 to 80 ppt in 1989 (Environment Canada 1991). By 1994, the content of PCB, dioxins, and DDE in herring gull eggs in the Great Lakes as a whole was reported to be 90% less than that measured in the late 1970s (Environment Canada 1994).

Table 1. The increasing rate of introductions of species to Lake Ontario (after Mills et al. 1993).

Time	No. of introduced species
1810–1839	1
1840–1869	15
1870–1896	26
1900–1929	22
1930–1959	33
1960–1990	41

As contaminants in eggs have decreased, the reproductive success of gulls, terns, and cormorants has increased. Rates of recovery are better documented than declines for most of these species. The decline of double-crested cormorants had reduced them to about 125 pairs in the Great Lakes in 1971 but their estimated numbers are now up to about 35 000 pairs (Prince et al. 1992; Environment Canada 1994). The interest of population dynamics of birds for habitat managers is threefold: low bird populations may need protection; the amount of predation may be limiting fish populations; and dense bird populations affect nutrient cycling, for example by adding nitrogen to reefs or small islands.

(L) Introduction of exotic species

The rate of introduction of exotic species has increased rapidly during the last century and a half (Mills et al. 1993). The rate is summarized in Table 1 for three-decade intervals for the Great Lakes.

Population dynamics of introduced species vary greatly. Some successful introductions remain rare while others become abundant. Plant species such as eurasian milfoil (*Myriophyllum spicatum*) can take one or two decades to become dominant, remain so for a decade and then decline (Crowder and Bristow 1986, 1988). Carp, alewife, and sea lampreys are also thought to have increased in abundance slowly (Sly 1991). At the other extreme are zebra mussels and quagga mussels (*Dreissena bugensis*), first reported in Lake Erie in 1985 and in Lake Ontario in 1989 (Schaner and Stewart 1994). A single settled *Dreissena* and some veliger larvae were found in the Bay of Quinte in 1990 and "major colonies" were reported from the bay by 1993. Densities now exceed 100 000 individuals·m^{-2} in the Trenton–Belleville area (Schaner and Stewart 1994). The mussels also occur at other sites in the Kingston Basin and in the St. Lawrence River.

Some introduced species have negligible effects on habitats while others greatly alter one or more of the physical, chemical, and biotic components. Invasive plants with strong impacts on habitats in the Kingston Basin include eurasian milfoil, frogbit (*Hydrocharis morsus-ranae*), and purple loosestrife (*Lythrum salicaria*) (White et al. 1993). They colonize submerged, floating-leaved, and emergent zones respectively.

Engel (1995) has summarized the impact of eurasian milfoil on fish habitats as follows:

"When dense, the plant obstructs swimming space of pelagic fishes, shelters too many juvenile fishes, and disrupts foraging movements of piscivores. In replacing native plants that harbor a diverse array of invertebrates, water milfoil cre-

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ates food shortages for fishes. By blocking sunlight penetration and water movements, it depletes dissolved oxygen inshore that can cause fish kill when shoots decay in autumn."

At present, zebra mussels have the greatest impact of any invasive animals. They have altered habitat structure by forming large colonies, have increased light penetration (Nicholls and Hopkins 1993), and presumably affect nutrient cycling. In Lake Erie, zebra mussels have caused major changes in food webs during the last decade, making the ecosystem "more benthic driven" (Haffner 1994).

Discussion and implications for management

The preceding review of shoreline habitats in the Kingston Basin shows that the physical, chemical, and biotic components have all undergone significant change, at a variety of spatial and temporal scales. All such changes impose a stress of some magnitude on the ecosystem. Many of these changes are anthropogenic but others are natural, suggesting that, even in the absence of human interference, the shoreline environment is not "constant and continuing." Therefore, given the existence of increasing financial constraints, the nature of the change must be analyzed carefully to determine whether management action is needed or possible.

Shoreline habitats in general are subject to more profound and rapid change than open lake settings. Shoreline areas are influenced by factors originating both from the lake as a whole (e.g., lake-level changes; lakewide water chemistry; introduction of exotic species) and from the surrounding land area (e.g., point-source contaminant loadings; sedimentation associated with construction activities). As a rule, stresses that originate from the adjacent land are likely to be more easily controlled by local management than those originating from the lake. Thus, it is useful to subdivide nearshore areas into those with greater or lesser amounts of terrestrial influence. For instance, wetlands in the estuarine reach of stream valleys are more susceptible to stresses from the land than wetlands within embayments without significant runoff. Similarly, the landward edge of a marsh is more likely to be adversely affected by terrestrial processes than the outer edge. It may then be more effective to devote local effort to those areas experiencing stress of terrestrial origin. Lakewide changes must be addressed in a different forum.

Of the many variables subject to change in nearshore habitats, physical factors (e.g., water-level changes; sedimentation and its influence on substrate character) and chemical factors (e.g., acidity, salinity, nutrient status, and contamination), together with the introduction of exotic species, are the primary external controls on the nature and behaviour of the ecosystem. Experience indicates, however, that changes in community structure brought about by a primary stress may trigger secondary changes in other components of the ecosystem, even though the other species are not seriously or even directly affected by the primary stress. Thus, cascade effects may occur because of the complex feedback relationships that exist between the various biotic components. For example, nutrient loading causing eutrophication in the Bay of Quinte led to increased turbidity, which then caused a decrease in macrophyte extent and biomass, accompanied by declines in the associated fauna. Managers need to consider these complex interactions, both in assessing the likely influence of a particular development and in deciding which of the many changes affecting an ecosystem are most in need of attention. Stresses with the greatest likelihood of compounded effects require more urgent action than those which influence only minor and isolated components of an ecosystem.

The rates of change displayed by physical, chemical, and biotic components of nearshore habitats in the Kingston Basin span several orders of magnitude, from the very slow rise in water levels associated with isostatic uplift of the lake outlet, to the nearly instantaneous change in acidity (acid shock) experienced by local areas during spring runoff. In general, slow change is more likely to be tolerated by an ecosystem. Thus, sedimentary data from the Cataraqui River estuary indicate that the wetland has existed more or less continuously over the last 4000 years, despite gradually rising lake levels (Fig. 3). Changes that are truly cyclic, such as annual variations in water levels, are also likely to be accommodated by the ecosystem, as long as the change stays within usual limits.

By contrast, the most important stresses are not cyclic. Instead, they are events that exceed the tolerance of the ecosystem, such as extreme low or high water levels, heavy sedimentation caused by nearby development, the introduction of a new contaminant, or the invasion of a rapidly proliferating, exotic species. Of the five types of ecosystem response discussed by Keith (1994), all have occurred in the shoreline habitats of the Kingston Basin. Examples of each include (*i*) continued functioning but with hiccups (piscivorous birds in response to the increase and subsequent decrease of contaminants); (*ii*) continued functioning but at a lower level (fish stocks in response to overfishing, contaminants, and exotic species; Fig. 6); (*iii*) incorporation of new features (introduction of carp); (*iv*) functions differently (algal communities in response to changing nutrient status); and (*v*) collapse without regeneration (the two episodes of marsh loss seen in the sediments of the Cataraqui River estuary; Fig. 3).

Responses of type *v* are clearly of greatest concern. In general, they are more likely to be caused by rapid, large-magnitude changes, but may also result from relatively small changes if the ecosystem or one of its important biotic components is already near the limit of its tolerance to a particular stress. Prior to reaching this threshold, the existence of a stress may cause only slight or slow change, but once this threshold is exceeded, catastrophic change takes place. The dramatic decrease in macrophyte biomass referred to already is a case in point.

In summary, habitat managers should be aware that shoreline habitats of the Kingston Basin have experienced almost continuous change and will continue to experience change in response to natural events and human action. Not all changes can or should be subject to intervention. Stresses originating from nearby land areas are most amenable to intervention, whereas those of lakewide origin cannot be controlled locally. Management action should focus on those changes with the greatest likelihood of compounded effects or of exceeding the adaption threshold of an ecosystem or an important component species.

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Possible impact of gobies and other introduced species on habitat restoration efforts

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Abstract: Many fish habitat modifications involve riprap placement on sandy substrate. Because exotic species may be favored, a field experiment was designed to test differences in fish abundance in riprap, sand, and macrophyte-dominated substrate. We used a 3-m long seine to sample areas of sand, riprap ($N = 5$ each), and aquatic macrophytes ($N = 2$) three times during 1994 in the St. Clair River near Algonac, Mich. Diversity was high, with 24 species of fish collected. Round gobies (*Neogobius melanostomus*) were most often collected in riprap and macrophyte habitat, with riprap habitat having a significantly greater mean catch on 16 August. On the other two dates, mean catches were not significantly different between macrophyte and riprap habitat, but both were significantly greater than the mean catch in sandy areas. Densities of tubenose gobies (*Proterorhinus marmoratus*) were similar between sandy and macrophyte habitats, but significantly greater in riprap habitat. Gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*), and white perch (*Morone americana*) were mostly associated with open water sandy habitat. Zebra mussels (*Dreissena polymorpha*) were common on riprap substrate but were rarely seen on sandy substrate. Fishery managers must be cautious in their selection of habitat modification choices to avoid favoring undesirable species.

Résumé : Beaucoup de modifications de l'habitat des poissons supposent la pose d'enrochements sur substrat sablonneux. Comme les espèces exotiques risques d'être favorisées par ce phénomène, nous avons conçu une expérience sur le terrain pour mesurer l'abondance respective du poisson selon l'habitat: enrochement, sable et substrat dominé par les macrophytes. Nous nous sommes servis d'une senne de trois mètres de long pour échantillonner des zones de sable, d'enrochements ($N = 5$ dans chaque cas) et de macrophytes aquatiques ($N = 2$) à trois reprises en 1994 dans la rivière Sainte-Claire à proximité d'Algonac (Michigan). La diversité était forte, puisque nous avons capturé 24 espèces de poisson. C'est le plus souvent dans les habitats à enrochements et à macrophytes que nous avons prélevé des gobies arrondies (*Neogobius melanostomus*), l'habitat dominé par les enrochements accusant une prise moyenne considérablement plus forte le 16 août. Les deux autres fois, la prise moyenne dans l'habitat dominé par les macrophytes ne différait pas sensiblement de celle que nous avons enregistrée dans l'habitat enroché, mais elle était dans l'un et l'autre cas nettement plus considérable que dans les zones sablonneuses. La densité de gobies de la mer Noire (*Proterorhinus marmoratus*) était la même dans l'habitat sablonneux que dans l'habitat dominé par les macrophytes, mais considérablement plus élevée dans l'habitat établi sur les enrochements. L'alose à gésier (*Dorosoma cepedianum*) le gaspareau (*Alosa pseudoharengus*) et le baret (*Morone americana*) étaient essentiellement associés à l'habitat sablonneux des eaux libres. Les moules zébrées (*Dreissena polymorpha*) étaient communes sur le substrat à enrochements, mais rare sur le substrat sablonneux. Les gestionnaires de pêches doivent choisir avec prudence leurs méthodes de modification de l'habitat pour éviter de favoriser les espèces indésirables.
[Traduit par la Rédaction]

Introduction

Many habitats throughout the Great Lakes, including wetlands, are being affected by construction activities in nearshore areas. As a result, there are now efforts underway or planned to restore areas to their former levels of productivity (Francis et al. 1979). Eroding beaches and slumping banks are sometimes stabilized using riprap or steel sheet piling, which encourages terrestrial plants to root, thereby assisting in erosion prevention. In other cases, building harbors, marinas, revetments, maintaining confined disposal facilities, and river control structures result in major modifications of fishery habitat (Kelso and Hartig 1995). If properly done, such activities can enhance productivity of some desired species or restore areas of concern (Holmes 1988; Hartig 1993). However, these projects are seldom evaluated for their effects on fish productivity nor is it ascertained which species are favored or disadvantaged.

Underwater studies of artificial reefs have shown that mottled sculpins (*Cottus bairdi*), yellow perch (*Perca flavescens*), and smallmouth bass (*Micropterus dolomieu*) are attracted to and fostered by habitat modification that adds riprap, steel piling, or other structures where only sand was previously found (Dorr and Jude 1980; Rutecki et al. 1985; Liston et al. 1985). Lake trout (*Salvelinus namaycush*) (Jude et al. 1981; Wagner 1981; Peck 1986), spottail shiner (*Notropis hudsonius*), yellow perch, and mottled sculpins also used these structure-enhanced substrates for shelter and spawning (Dorr and Jude 1980). Often, no consideration is given to how habitat modification enhances opportunities for introduced species, nor is the ecology of potential invaders evaluated before

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Table 1. Compilation of the mean catch (no./10 m^2) of fish species collected through seining from three habitat types along shore in the St. Clair River, Algonac, Mich.

	3 June			28 June			16 August		
Species	Sa	Ri	Ma	Sa	Ri	Ma	Sa	Ri	Ma
Bluntnose minnow	0.0*a*	0.2a	17.0*b*	0.1*a*	0.4*ab*	2.1*b*	0.0*a*	0.0*a*	0.0*a*
Channel darter	0.0	0.0	0.0	0.2	0.2	0.5	0.0	0.4	0.0
Emerald shiner*	0.0	0.0	0.0	2.8	0.3	3.5	2.6	0.0	0.0
Rainbow darter*	0.1	0.3	0.3	0.1	1.6	0.3	0.0	1.1	0.0
Rainbow smelt*	3.4	0.0	0.0	7.4	2.7	14.1	0.0	0.0	0.0
Round goby	0.0*a*	2.1*b*	2.9*b*	0.0*a*	6.9*b*	5.3*b*	0.2*a*	3.8*b*	0.5*a*
Sand shiner	0.0	0.0	0.0	0.2	0.1	0.3	0.0	0.0	0.0
Smallmouth bass	0.0	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
Spottail shiner*	0.1	0.0	0.5	1.8	0.4	1.9	0.1	0.1	0.0
Tubenose goby*	0.1	0.7	0.3	0.0	1.0	0.0	0.0	0.0	0.0
White perch	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.2	0.0
White sucker	0.0	0.0	0.0	0.0	1.2	0.8	0.0	0.0	0.0
Total no. of species	4	7	5	11	12	10	7	6	1
No. of fish (all species)	3.7	3.8	21.0	13.0	15.2	29.1	5.4	5.7	0.5

Note: Samples were collected on 3 June, 28 June, and 16 August 1994. There were five replicates for sandy (Sa) and riprap (Ri) and two for macrophyte (Ma) habitat. Common names according to Robins et al. (1980). Mean catches with similar letters are not significantly different ($P > 0.05$), while those with different letters are different. Totals include 12 rare species mentioned in text.

*These species, which appear in Table 2, had pooled tests performed on means. All remaining comparisons were not significant.

rehabilitation is attempted. Such information is necessary to guide decisions about the types of modifications proposed and to predict the responses of various species as a result of choosing modifications available. In this study, an attempt was made to document variations in species abundance with respect to presence or absence of riprap and its implications for fostering the newly introduced tubenose (*Proterorhinus marmoratus*) and round gobies (*Neogobius melanostomus*) (Jude et al. 1992). We did this by comparing catches in sandy, riprapped, and vegetated areas in the St. Clair River.

Methods

A field experiment was designed to compare catch rates of round gobies and other fishes along the St. Clair River in adjacent areas of three differing habitat types. One of these areas was riprapped with rock-filled, wire gabions. Another was an extensive area of sandy beach, and the third was a small area of macrophyte-covered substrate, located between the sandy and riprapped areas. A backpack electroshocker was used to collect fishes in 1993 and proved unsuccessful, because shocked gobies tended to remain on the bottom (they have no swim bladder) and were difficult to see in often turbid conditions. Therefore, a 4.7 m long by 1.4 m high bag seine with 6 mm bar mesh was used, since it proved more efficient. The bag was 1.2 m wide by 1.5 m deep. Seining covered an area of approximately 18.8 m^2. An attempt was made to sample that amount of area in sand, riprapped, and macrophyte-covered substrates. In the sandy area, we placed the seine about 4 m from the shore and seined perpendicular to shore. This was repeated five times in the sandy substrate, but only twice in the macrophyte-dominated (sparse growth of *Chara*, *Potamogeton* spp., *Vallisneria*) substrate, because macrophytes only existed in a small area of the river at our study site. In the riprap area, because of snagging difficulties, the seine was placed about 4 m from shore. Two people held the seine while a third kicked rocks and substrate, which scared fish into the current-filled bag of the seine (five replicates were completed using this procedure). Fishes from each replicate haul were placed in individually labeled containers; samples from 3 June were preserved in alcohol, while the rest were frozen. Sampling resulted in the collection of 12 aggregate samples per trip. This sampling scheme was repeated three times: 3 June, 28 June, and 16 August 1994. After collection, fish were brought to the laboratory and weighed to the nearest 0.01 g, and total length was measured to the nearest mm.

Catch data were analyzed using a two-factor ANOVA with the factors being "date" and "location." Data were transformed using a square root transformation to better meet the assumptions of normality. If significant ($P < 0.05$) main effects were found, means were compared using the Tukey simultaneous multiple comparison technique. If a significant interaction was found, comparisons among location means were performed for each sampling date using the Bonferroni simultaneous multiple comparison technique. There were unequal replicates (two vs. five) across habitat types; however, the multiple comparisons utilized the mean square error of the overall test, which is derived from the replicate variability within all cells (location within date). The cell variances of square-root transformed data did not appear to be heterogeneous.

Results

The nearshore zone of the St. Clair River contained a diverse fish community, based on our collection of 641 fish of 24 different species during our 1994 study (Table 1). Twelve fish species were collected only in one habitat type and in low (0.1–1.1/10 m^2) densities: sand (alewife, *Alosa pseudoharengus*, 1.1; gizzard shad, *Dorosoma cepedianum*, 1.0; johnny darter, *Etheostoma nigrum*, 0.1; longnose dace, *Rhinichthys atratulus*, 0.1; muskellunge, *Esox masquinongy*, 0.1), rip rap (chinook salmon, *Oncorhynchus tshawytscha*, 0.1; logperch, *Percina caprodes*, 0.1; mottled sculpin, 0.1; rock bass, *Ambloplites rupestris*, 0.1; yellow perch, 0.2), and macrophytes (hornyhead chub, *Nocomis biguttatus*, 0.3). Rainbow smelt (*Osmerus mordax*) and bluntnose minnows (*Pimephales notatus*) were the two most abundant fishes in collections, while round gobies, rainbow darters (*Etheostoma caeruleum*), and spottail shiners had the highest frequencies of occurrence, being found at seven of the nine habitat–date combinations. Highest mean total catches (all species combined) and species

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Table 2. Statistical comparisons of catches (no./10 m^2) among habitat types and dates for species and total catches for which no interactions allowed testing of means pooled over respective habitats or dates.

	Sand	Riprap	Macrophytes	3 June	28 June	16 August
Emerald shiner	1.8*a*	0.1*b*	1.2*ab*	0.0*c*	1.9*d*	1.1*cd*
Rainbow darter	0.1*a*	1.1*b*	0.2*a*	0.3*c*	0.8*c*	0.4*c*
Rainbow smelt	3.6*a*	1.2*a*	4.7*a*	1.4*c*	7.0*d*	0.0*c*
Spottail shiner	0.7*a*	0.2*a*	0.8*a*	0.1*c*	1.3*d*	0.1*a*
Tubenose goby	0.0*a*	0.6*b*	0.1*a*	0.4*c*	0.4*c*	0.0*c*
All species combined (3 June)	3.7*a*	3.9*ab*	21.0*b*	—	—	—
All species combined (28 June)	13.1*a*	16.2*a*	29.0*a*	—	—	—
All species combined (16 August)	5.3*a*	5.7*a*	0.5*a*	—	—	—

Note: Fish were collected in 1994 by seine in the St. Clair River near Algonac, Mich. Mean catches with similar letters are not significantly different ($P > 0.05$). Sample sizes were 15 each for sand and riprap, 6 for macrophytes, and 12 for each of the date comparisons.

diversity occurred during the 28 June 1994 sampling event, but mean total catch differences among habitat types were only statistically significant ($P < 0.05$) for the 3 June trip (Table 2). On this date, mean total catch was higher in the macrophyte area than in the sandy area, but mean catch in the macrophyte area was not significantly different from mean catch in the riprap area (Table 2). Catches from sandy and riprap areas were similar. Riprap also generally had highest species diversity among the three habitat types, with highest numbers of species occurring during 28 June and 16 August. Round gobies were most often collected from riprap and macrophyte habitats, with riprap habitat having significantly higher mean catch rate during the 16 August period (Table 1). On the other two dates, mean catches from the macrophyte and riprap habitat were not significantly different, but both had significantly higher mean catch rates than those measured in sandy areas. In fact, during the day, no round gobies were collected on sandy substrate on 3 and 28 June, and very few were collected there on 16 August.

In addition to the round goby, six other exotic species were collected. Mean catches of tubenose gobies were similar between sandy and macrophyte habitats but significantly higher in riprap habitat (Table 2). For rainbow smelt, catches were similar among habitat types, with a tendency of fish to be associated with sand. Chinook salmon, white perch (*Morone americana*), and alewife mean catches were not significantly different among habitat types or dates, mainly due to low sample size. Alewife, gizzard shad, and white perch were mostly associated with sand and were not collected at other sites. Gizzard shad catches were also small, with the only significant differences being on 16 August when mean catch in sandy habitat was higher than observed in the other two habitats.

One endangered species, the channel darter (*Percina copelandi*), was also collected. It was found in all three habitat types on 28 June and in the riprap site on 16 August. The only mottled sculpin collected was associated with riprap. Rainbow darters, too, were significantly more abundant in the riprap than in sandy or macrophyte habitats; catches in these two latter habitats were not significantly different from each other (Table 1).

During these collections and others during 1992–1995, we examined many pieces of riprap and stones for the presence of zebra mussels (*Dreissena polymorpha*) and found them to be common on the undersides of riprap along the bulwarked shoreline. In contrast, the sandy, open-water areas had no accumulation of zebra mussels on the bottom; zebra mussels were only observed attached to stones and other hard objects in the water.

Discussion

The physical environment sets bounds for the biological communities that develop within them and is an important predictor of the fish and invertebrate species that will flourish in an aquatic ecosystem. Jude and Pappas (1992) showed a trend of decreasing fish species diversity along a gradient of decreasing habitat quality from individual Great Lakes to degraded coastal wetlands. For example, shallow, densely vegetated, and eutrophic parts of a lake may provide ideal habitat for common carp (*Cyprinus carpio*) (McCrimmon 1968), while sandy beach areas are important nursery areas for minnows and other species of fish (Heufelder et al. 1982; Madenjian and Jude 1985). Rocky substrates may enhance the survival of mottled sculpins, bluntnose minnows, and johnny darters, which build and guard nests on the undersides of rocks, logs, and other structures (Scott and Crossman 1973). Because so much valuable fishery habitat is lost or altered, fishery managers now restore or rehabilitate habitat degraded by excessive nutrients, toxic substances, infilling, and physical changes resulting from construction of various structures (Kelso and Hartig 1995). Obviously, fish that spawn in pelagic waters, such as alewife, gizzard shad, and white perch, those that deposit eggs over sandy substrate, such as logperch, spottail shiners, rainbow smelt, and sand shiners (*Notropis stramineus*), or those that defend nests built on sandy substrate would be little affected by placement of typical riprapped structures, unless they were placed over optimal sediment types or created these substrates in areas where they were formerly limiting. However, if placement of riprap or other structures would favor the development of sheltered areas or macrophytes, species such as brook silverside (*Labidesthes sicculus*), yellow perch, and longnose gar (*Lepisosteus osseus*), which spawn over or use vegetation (Scott and Crossman 1973), would benefit by such a development, particularly if this type of habitat was limiting. Vegetated habitats are more important to most fishes than are open areas (Eadie and Keast 1984; Conrow et al. 1990; Dewey and Jennings 1992). However, one drawback is that juvenile zebra mussels can also grow on aquatic macrophytes (Lewandowski 1983), which would provide additional food resources for round gobies.

Exotic species of fish are an increasing threat to native fish

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communities in all the Great Lakes, and species such as the alewife have caused cascading effects through affected food chains (Scavia et al. 1986). Other exotic species, such as the ruffe (*Gymnocephalus cernuus*) in Lake Superior (Pratt et al. 1992), are expanding their range, and other invertebrates, such as the zebra mussel (Hebert et al. 1989), have wrought dramatic changes in water clarity and the ecology of several water bodies in the Great Lakes and beyond (Leach 1992; Holland 1993), including effects on enriching the benthos (Dermott et al. 1992; Griffiths 1992). It is well known that zebra mussels attach to most hard substrates and even macrophytes (Leach 1992; Kilgour and Mackie 1992; Martel et al. 1994). Leach (1992) and Fitzsimons et al. (1995) found that zebra mussels did not negatively affect walleye (*Stizostedion vitreum*) spawning success on traditional spawning reefs colonized by zebra mussels. However, they kill many native unionid clams on which they attach (Hebert et al. 1991; Nalepa 1994). Using trawls, we captured large numbers of zebra mussels that were unattached to substrate but had still formed druses by attaching to each other, or had strung themselves together in long strands (D. Jude, unpublished data). The newest member of the dreissenid group, the quagga mussel (*Dreissena bugensis*), has extended its range into deeper waters of the Great Lakes than did the zebra mussel and can flourish in lower water temperatures than its congener (Rosenberg and Ludyanskiy 1994; Spidle et al. 1994). Availability of quagga mussels in deeper water may favor the spread of round gobies away from preferred nearshore areas.

The round goby is a recent addition to the Great Lakes fish fauna (Jude et al. 1992) and is currently found throughout the St. Clair River and the upper reaches of the Detroit River and has established populations in the Grand River, Lake Erie, the Grand Calumet River in southern Lake Michigan (Jude et al. 1995), and most recently in Lake Superior (J. Selgeby, National Biological Service, Ashland, Wis., personal communication). In its native Black Sea habitat, the round goby is found in slow rivers, lagoons, and brackish coastal waters to 20 m (Miller 1984), while the tubenose goby has adapted to lentic environments, especially ponds overgrown with submerged vegetation (Lelek 1980). Round gobies are not expected to become abundant in nearshore areas of the Great Lakes, including Lakes Michigan and Huron, where sand bottoms predominate. However, there are reports from fishermen of round gobies in 15 m of water near a shipwreck site in southern Lake Michigan and from 12 m of water in the central basin of offshore Lake Erie (K. Muth, National Biological Service, Sandusky, Ohio, personal communication). From the Grand Calumet River it now has access to the Mississippi River and connecting waters. Our work shows that this species has severely depressed and displaced populations of mottled sculpins in the St. Clair River and diminished populations of benthic species such as the logperch. This study and that of Jude et al. (1995) show that round gobies prefer and flourish in areas of rock, cobble, riprap, and vegetation in the nearshore margins of rivers. Round gobies are not confined to these areas; they can also be found throughout the St. Clair River, including the channel, although in lesser densities (D. Jude, unpublished data). Habitat enhancement projects can restructure a fish community because these projects may provide ideal habitat for the reproduction and expansion of round gobies, which prefer large interstitial spaces among rocks for refuge and spawning. These projects will also supply hard substrate for attachment of zebra mussels, which are an important food for larger round gobies (Jude et al. 1995); other species are not known to have exploited zebra mussels to the extent that round gobies have (French and Burr 1992; French 1993).

Therefore, fish managers should be aware of the potential effects of fish enhancement projects that may provide round gobies with advantages over desired native species. This concern should not be restricted only to their current range but also to areas of future range expansion, including Duluth–Superior Harbor in Lake Superior and inland lakes.

The effects of exotic species introductions and, therefore, the effects of habitat changes that favor them can have far-reaching impacts on fish communities. Modifications to the Welland Canal and subsequent sea lamprey (*Petromyzon marinus*) depredations have had devastating permanent effects on Great Lakes ecosystems (Smith 1973; Christie 1974). Zebra mussel mediated changes in water clarity and quality (e.g., Holland 1993; Fahnenstiel et al. 1995), proliferation of nongrazed algae and increases in macrophytes (Skubinna et al. 1995; Lowe and Pillsbury 1995), and decreases in rotifer and zooplankton populations (T. Nalepa, Great Lakes Environmental Research Laboratory, Ann Arbor, Mich., personal communication) may have led to yellow perch recruitment failure in Saginaw Bay, Lake Huron (R. Haas, Michigan Department of Natural Resources, Mt. Clemens, Mich., personal communication). It is, therefore, incumbent upon all fish managers to examine any modifications in fishery habitat to insure that such well meaning activities do not favor undesirable species to the detriment of desirable ones.

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The significance of man-made structures for lake trout spawning in the Great Lakes: are they a viable alternative to natural reefs?

John D. Fitzsimons

Abstract: High lake trout (*Salvelinus namaycush*) egg abundance reported at some man-made structures, including artificial reefs in Lakes Michigan and Ontario, indicates that construction of artificial reefs may be one means of enhancing reproduction for this species in the Great Lakes. A review of spawning at man-made and natural spawning areas indicated consistently higher abundance of eggs, fry, and young-of-the-year lake trout associated with man-made structures. Hence, artificial reefs could make a significant contribution to restoration of lake trout stocks in the Great Lakes. It was not clear, however, why some man-made structures were used by lake trout and some were not. It is recommended, therefore, that construction of artificial reefs be approached on an experimental basis and that reef construction be part of an overall strategy to increase availability of spawning habitat. Also included in this strategy is stocking lake trout closer to areas of natural spawning substrate and resolving potential resource user conflicts. Studies should also be conducted to evaluate how life stage at stocking (e.g., egg, fry, yearling) affects subsequent use of spawning habitat and to determine if genetic factors are involved.

Résumé : Compte tenu de la considérable abondance d'oeufs de touladi (*Salvelinus namaycush*) signalée près de certains ouvrages fabriqués par l'homme, et notamment des récifs artificiels dans les lacs Michigan et Ontario, on peut supposer que la construction de récifs de ce genre constitue un moyen d'améliorer la reproduction de cette espèce dans les Grands Lacs. En étudiant la reproduction dans les frayères artificielles et naturelles, nous avons constaté que les oeufs, les alevins et les jeunes de l'année étaient toujours plus abondants près des ouvrages artificiels. Les récifs artificiels pourraient donc faire beaucoup pour la reconstitution des stocks de touladi dans les Grands Lacs. Nous n'avons cependant pas pu déterminer la raison pour laquelle certains ouvrages artificiels étaient utilisés par le touladi et d'autres non. Nous recommandons donc d'envisager la construction de récifs artificiels sous l'angle expérimental, et de l'entreprendre dans le cadre d'une stratégie globale visant à agrandir l'habitat de reproduction. Cette stratégie consisterait également à ensemencer du touladi plus près des zones de substrat naturel de reproduction et à résoudre les conflits éventuels entre les utilisateurs de la ressource. Il faudrait aussi entreprendre des études pour voir en quoi le stade biologique au moment de l'empoissonnement (p. ex., oeuf, alevin, sujet d'un an) influe sur l'utilisation ultérieure de l'habitat de reproduction, et pour déterminer le rôle éventuel de facteurs génétiques.
[Traduit par la Rédaction]

Introduction

Artificial reefs have been used since the 1800s as a fisheries management tool in both the freshwater and marine environments (Stone 1985). Their ability to increase fish abundance and biological productivity has received considerable attention although less is known about their ability to function as spawning substrates particularly for lake trout (see D'Itri 1985).

The first use of artificial reefs to enhance lake trout reproduction in inland lakes was in the 1950s. Reefs were constructed to provide alternate spawning habitat, either for protection from predation by fish (Prevost 1956), or amphibian (Hacker 1957) egg predators, or for habitat lost to the effects of water drawdown (Martin 1955). In all instances there was at least some measure of success in improving lake trout reproduction.

More recently, artificial reefs have been constructed in Lakes Michigan (Kevern et al. 1985), Huron (Foster and Kennedy 1995), and Ontario (Gannon et al. 1985) with the intention of providing spawning habitat for lake trout where natural spawning habitats were generally scarce. Although lake trout were observed in the area of each reef, the only evidence of spawning was at the Tawas reef site in Lake Huron. Lake trout spawning has also been noted on other man-made structures, including water intakes, breakwalls, and artificial reefs in all of the Great Lakes with the exception of Lake Erie (Jude et al. 1981; Wagner 1981; Nester and Poe 1984; Peck 1986; Fitzsimons 1994*a*, 1995; Marsden 1994; Schreiner et al. 1995). Clearly, under certain circumstances, artificial reefs that attract lake trout and have the potential to improve lake trout reproduction can be constructed.

Reproduction by lake trout in most of the Great Lakes continues to be poor (Dorr et al. 1981; Jude et al. 1981; Wagner 1981; Nester and Poe 1984; Marsden et al. 1988), although based on intensive surveys at a number of spawning reefs it appears unrelated to numbers of fish stocked or the quality of

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their gametes (Selgeby et al. 1995; Fitzsimons 1995; Fitzsimons et al. 1995). Studies in Lakes Michigan and Ontario that measured egg densities indicated little use of the scant natural spawning habitat available although considerable use of man-made structures in these lakes has occurred (Marsden 1994; Fitzsimons 1995). This implies that man-made structures that include artificial reefs may be a viable option for improving natural reproduction.

The purpose of this review is to *(i)* examine the need to build artificial reefs for lake trout spawning in the Great Lakes, *(ii)* compare spawning use at man-made structures relative to natural spawning reefs, *(iii)* compare habitat features at man-made structures with those at natural spawning reefs, *(iv)* determine what factors were involved in lake trout spawning at artificial reefs and man-made structures, (*v*) indicate what habitat features are important in the design of either man-made structures or artificial reefs to enhance their use by spawning lake trout, and (*vi*) provide recommendations for the use of artificial reefs and man-made structures to enhance lake trout reproduction in the Great Lakes.

Is there a need for artificial reefs in the Great Lakes?

Information available on direct losses of lake trout spawning habitat in the Great Lakes is very limited but these losses could be quite significant at least in Lake Ontario. Stone hooking operations from Hamilton to Toronto resulted in the loss of virtually all cobble substrates and the elimination of at least four lake trout spawning reefs (Whillans 1979). As a result, spawning habitat in this area now appears to be limited to man-made structures associated with shoreworks, although none of these were built expressly for lake trout (G. MacPherson, Metropolitan Toronto Region Conservation Authority, Toronto, Ont., personal communication; J. Fitzsimons, unpublished observations).

Compared with direct losses of spawning habitat, what are in effect indirect losses may have been more pervasive and contributed to a greater reduction in availability of spawning habitat in the Great Lakes. Although these indirect losses did not cause an actual loss in quantity of spawning habitat they resulted in a loss of habitat availability through a combination of factors including loss of genetic strains, fish-stocking practices, and behaviour.

Historical inference, based on the association of large catches of spawning condition adult lake trout with specific habitat types, was that lake trout spawned on a wide variety of substrate types, including cobble, rubble, clay, and honeycombed bedrock that were found over a wide range of depths in the Great Lakes including some rivers draining into Lake Superior (Loftus 1957; Goodier 1981; Goodyear et al. 1982*a*, 1982*b*, 1982*c*, 1982*d*, 1982*e*; Thibodeau and Kelso 1990). In contrast, spawning by contemporary lake trout stocks appears restricted to cobble substrates in relatively shallow (< 15 m) water (Jude et al. 1981; Wagner 1981; Peck 1986; Marsden and Krueger 1991; Fitzsimons 1994*a*, 1995; Casselman 1995; Holey et al. 1995; Kelso et al. 1995; Schreiner et al. 1995). The difference between historic and contemporary accounts may result from incorrectly inferring where spawning occurred. Alternatively, spawning habitat site selection may have become less diverse as a result of the loss of genetic strains that spawned at greater depths or used spawning habitat other than cobble. Brown et al. (1981), Goodier (1981), and Dehring et al. (1981) suggested that some of the reported historic variability in spawning habitat selection was the result of multiple strains of lake trout that occurred historically in the Great Lakes. Some historic strains apparently spawned at depths > 15 m to as much as 80–90 m in Lakes Michigan and Huron and up to 180 m in Lake Superior (Thibodeau and Kelso 1990). Spawning by contemporary stocks of lake trout in Lake Tahoe at depths of 40–60 m that are descendants of historic stocks collected in 1889 at Julians Reef in southwestern Lake Michigan provides circumstantial evidence for the historic occurrence of deep-spawning strains of lake trout at least in Lake Michigan (Beauchamp et al. 1992). Many of the historic native strains, however, were lost when lake trout became extinct in the Great Lakes in the 1950s and 1960s, with the exception of Lake Superior and parts of Georgian Bay. Some deep-spawning strains may still exist in Lake Superior as indicated by the presence of spawning condition siscowets, a lake trout subspecies, on spawning reefs at depths in excess of 20 m (J. Peck, Michigan Department of Natural Resources, Marquette, Mich., personal communication). The loss of deep-spawning stocks has, in effect, meant a "loss" of spawning habitat as contemporary stocks appear to prefer shallow spawning areas in lakes Michigan (Marsden 1994) and Superior (Hansen et al. 1995).

Stocked fish, regardless of strain (Perkins et al. 1995), tend to return to shallow areas along the shore where they were stocked to spawn (Brown et al. 1981). In the Apostle Islands area of Lake Superior, where most spawning habitat is offshore and associated with islands, Krueger et al. (1986) found there were higher returns of wild than stocked fish. The low returns of stocked fish led these authors to conclude that stocked fish were reproductively ineffective. However, recent studies in the Minnesota and Michigan waters of Lake Superior where spawning habitat is abundant nearshore have indicated that stocked lake trout were largely responsible for stock recoveries (Hansen et al. 1995). These findings, using a broader geographical area, in contrast to those of Krueger et al. (1986), imply instead that stocked fish can spawn successfully but that they have a predilection for shallow nearshore waters. Efforts to circumvent this tendency to spawn in shallow water by stocking at deeper and more remote offshore reefs has not been very successful based on work in Lake Huron. Bowen et al. (1994) reported that the highest catch per unit effort of mature lake trout on Six Fathom Bank, which were stocked there as juveniles, occurred at the shallowest depths of this relatively deep offshore reef complex.

Part of the tendency of stocked lake trout to spawn in shallow nearshore water may, however, be unrelated to cultural factors. Kelso et al. (1995) reported shoreline spawning by mixed stocks of wild and stocked lake trout in depths of < 5 m along the north shore of Lake Superior indicating that this behaviour may be an innate characteristic of the species. Eshenroder et al. (1995) suggested that shallow water spawning by lake trout was the result of evolution in small inland lakes where the main source of spawning substrate was shoreline erosion.

The preference by spawning lake trout for nearshore areas of the Great Lakes may result in low spawning success due to the combined effects of the geology of the Great Lakes and

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current stocking practices. In the Great Lakes, cobble size substrates at shallow depths and nearshore are spatially heterogenous (Sly and Thomas 1974; Edsall et al. 1989). This substrate size, which is largely the result of glacial activity, is only abundant along the north and south shores of Lake Superior, and northern shores of Lakes Michigan, Huron, and Ontario. However, even in those areas where cobble is abundant, relatively little may be suitable for spawning by lake trout. At Gull Island Shoal, one of the most significant offshore reef complexes in Lake Superior (Swanson and Swedberg 1980), only 2% of a 2000-ha area was judged to have excellent quality in terms of rock size and depth of interstices based on visual and side-scan sonar substrate evaluation (G. Kennedy, National Biological Service, Ann Arbor, Mich., personal communication). Use of existing cobble substrate by spawning lake trout may be reduced even further by selection for cobble substrates with a minimal depth of interstices and associated with a steep drop-off (Marsden and Krueger 1991; Fitzsimons 1994*a*, 1995). At Stony Island, a natural spawning reef in Lake Ontario, Marsden and Krueger (1991) found using egg density, a better indicator of spawning activity than the presence of cobbles that can only be used to infer a potential for spawning, that only 5% of the reef had the requisite spawning characteristics.

As a result of the heterogenous distribution of spawning habitat in the Great Lakes construction of artificial reefs may provide critically important lake trout spawning substrate in some areas. In southern and central Lake Michigan, where cobble substrates are rare nearshore, man-made structures have been the only sites where substantial numbers of lake trout eggs and fry have been collected (Jude et al. 1981; Wagner 1981; Marsden 1994; Holey et al. 1995). In Lakes Superior and Ontario also, studies have indicated that the highest density of lake trout eggs occurs on man-made structures in areas where natural cobble substrates are rare (Marsden 1994; Schreiner et al. 1995; Fitzsimons 1995).

Stocking sites for hatchery-reared lake trout relative to spawning habitat may impose an additional constraint on the use of limited spawning habitat. Lake trout have an ability to recognize and use suitable substrates, either natural or man-made that are some distance away from stocking sites (Fitzsimons 1994*a*; Perkins et al. 1995) although the area searched may be restricted by home range. For lake trout home range has been estimated at 300 000 ha, which would be equivalent to a 60-km radius around a stocking site (Ihssen et al. 1988). As stocking locations are selected in part to provide sport fishing opportunities (Schneider et al. 1983) and to reduce effects of impacts from commercial fisherman and lamprey predation, stocked lake trout may not find suitable spawning habitat within their home range for a particular stocking location. As a result lake trout may spawn on cobble that is unsuitable due to inadequate water depth or excessive sediment infilling of interstices resulting in increased egg and fry mortality (Manny et al. 1989; Fitzsimons 1994b).

A review of lake trout spawning at man-made structures and natural spawning areas in the Great Lakes

Many of the sources of information available on lake trout spawning in the Great Lakes relied upon indirect historic evidence. As such, there is uncertainty as to where lake trout actually spawned (Thibodeau and Kelso 1990). Much of this indirect information came from observations by commercial gillnet fisherman of large numbers of mature spawners in the vicinity of potential spawning reefs. Using these observations, which are largely anecdotal, 827 lake trout spawning reefs were documented in the Laurentian Great Lakes (Thibodeau and Kelso 1990). Although this information implies spawning activity it does not demonstrate it since fish may be en route to a spawning site. Moreover, Fitzsimons (1995) found that based upon visual evaluation of 14 historically important spawning reefs in Lake Ontario, only five had a high potential for spawning based on the presence of suitable spawning substrate (Wagner 1981; Peck 1986; Marsden and Krueger 1991; Fitzsimons 1994*a*). Many contemporary investigators have experienced similar difficulties in identifying active spawning areas based on gillnet catches (Peck 1975, 1977, 1979; Wagner 1982; Kelso et al. 1995). Hence, the only direct evidence of spawning by lake trout accepted by this author is the collection of eggs, fry, or young-of-the-year (YOY). Accordingly direct observations alone are used in the following review of spawning at man-made and natural spawning areas in the Great Lakes.

It is difficult to readily compare spawning activity at man-made structures to natural reefs in the Great Lakes because of the diversity of methods used to collect lake trout eggs and fry. These methods have included active gears such as suction samplers and trawls (Stauffer 1981), and numerous passive sampling gears including egg pails (Stauffer 1981), egg trays (Sly 1988), egg bags (Horns et al. 1989), egg traps (Marsden et al. 1991: Perkins and Krueger 1994*a*), egg nets (Perkins and Krueger 1994*b*), egg funnels (J. Fitzsimons, unpublished data), and fry traps (Stauffer 1981). The use and limitations of these different methods has received considerable review (Stauffer 1981; Fitzsimons 1994*a*; Kelso et al. 1995; Schreiner et al. 1995). What little comparative work has been done between methods indicates considerable variation that can result in qualitative and quantitative differences in evaluation of egg deposition (Perkins and Krueger 1994*a*). Accordingly, while some gears may provide quantitative estimates of egg density, others may be limited to relative catch per unit of effort. In addition, for the same gear, considerable spatial variation is evident, even on small reefs (Peck 1986; Marsden and Krueger 1991; Fitzsimons 1995). Whether this variation results from spatial variation in spawning activity or some other factor that influences catchability, such as currents or proximity to a drop-off, is not known. Active gears such as pumps and airlifts used during or after spawning present additional difficulties in obtaining quantitative samples of egg deposition. Samples must be taken right after spawning occurs before eggs settle too deeply into the interstices where sampling by surface-operated pumps is not quantitative. Although SCUBA divers can more effectively sample eggs entrained in interstices by excavating spawning substrate using airlifts, in deep (> 1 m) substrates many eggs may settle below a practical working depth for this gear.

Given the limitations on some collection methods comparisons of lake trout spawning between man-made structures and natural spawning areas were generally restricted to those studies that used egg nets, egg pails, egg trays, egg traps, and egg bags. Egg abundance using the first three gears was expressed

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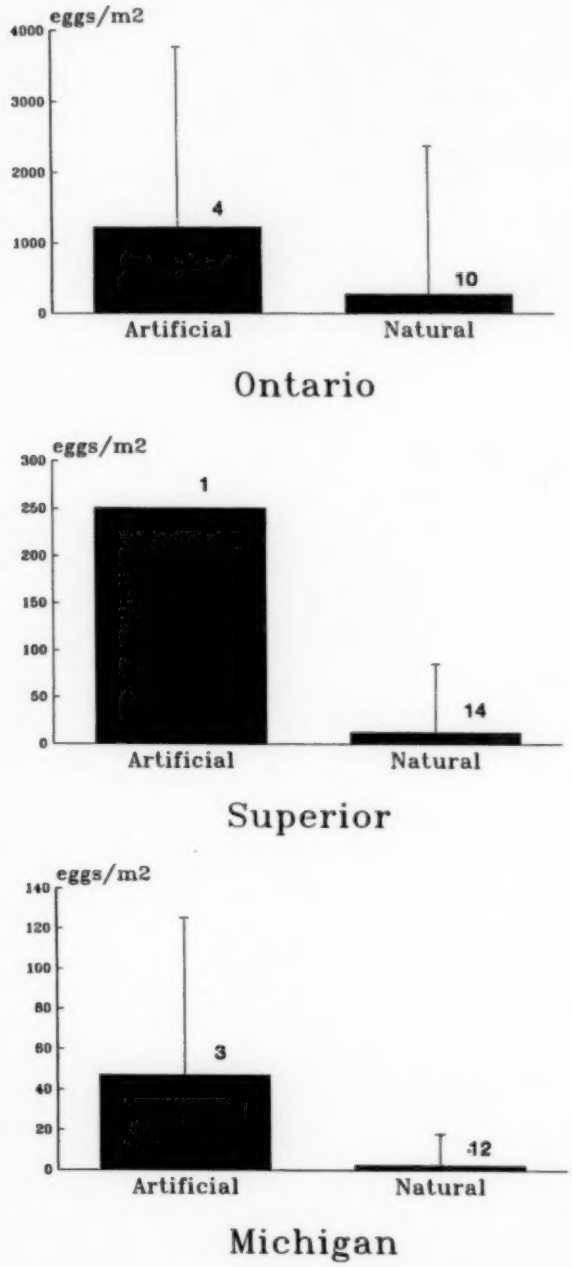
Fig. 1. A comparison of lake trout egg abundance (eggs per square metre; mean and range) at artificial and natural spawning areas in Lakes Ontario, Superior, and Michigan using various collection gears. Number of individual sites used to calculate the mean is shown beside the range bar. Data are from Dorr et al. (1981), Wagner (1981), Peck (1986), Marsden et al. (1995*b*), Marsden and Krueger (1991), Casselman (1991), Fitzsimons (1995), Perkins and Krueger (1995), Kelso et al. 1995, and Wagner 1981.



as eggs per square meter, while for traps and bags abundances were calculated as eggs per 1000 trap days and eggs per 1000 bag days, respectively. Comparisons between man-made structures and natural spawning areas were only made using gears for which abundance could be calculated on the same basis. For some lakes where samples were collected right after spawning with egg pumps, egg abundance was expressed as eggs per square meter. Collections of fry were restricted to those made with emergent fry traps and expressed as fry per square meter over the period of emergence and catches of YOY lake trout were made exclusively with trawls (e.g., otter, beam) and expressed as YOY per 1000 square meters. Data for 60 spawning areas in the Great Lakes was reviewed, 18 of which were man-made structures. Spawning areas were located in Lake Michigan (22), Lake Ontario (18), Lake Superior (12), and Lake Huron (8). There is no information as to where lake trout spawn in Lake Erie. The large number of known spawning areas evaluated in Lakes Ontario and Michigan (Marsden 1994; Fitzsimons 1995) reflects the attempts to determine the causes of poor natural reproduction (Elrod et al. 1995; Holey et al. 1995). Comparisons of spawning activity between man-made structures and natural spawning areas for each of Lakes Ontario, Huron, Michigan, and Superior are depicted in –5. These five figures clearly indicate that spawning and survival to the emergent fry and YOY stage can be significant at man-made structures.

In all comparisons involving collections of eggs at man-made structures and natural spawning areas, the number of eggs collected, whether with egg nets, traps, pails, bags, trays, or pumps, was higher at man-made structures, by 4.5–200 times (Figs. 1–3). For Lake Huron the estimate of numbers of emergent fry at a man-made structure was 1.3 times higher than at a natural spawning area (Fig. 4). Emergent fry abundance averaged 24·m^{-2}, based on two man-made structures in Lake Michigan, although no fry were detected at four natural spawning areas.

Few measures of YOY have been made in the Great Lakes although estimates indicate that higher numbers of YOY are also associated with man-made structures than natural spawning areas. Catches of YOY at two man-made structures in Lake Superior were 59 times higher than at a natural spawning area in this lake (Fig. 5). A mean of 5.5 YOY·1000 m^{-2} was calculated for seven man-made structures in Lake Michigan, but no YOY were collected at seven natural spawning areas sampled in this lake.

Considerable variation was evident in the data used to compare man-made structures with natural spawning areas. Variation in the biological and physical characteristics at the sites along with the inherent limitations of the collection methods used have probably all affected catchability. Although all of the gears used can indicate lake trout spawning, there is less certainty about the absence of spawning when no eggs, fry, or YOY are collected. Accordingly, caution should be used in drawing conclusions, although given the consistency in the observations using several methods to sample eggs, fry, and YOY in several lakes, data indicate that the differences are real.

There are several reasons why man-made structures may have higher abundances of eggs, fry, or YOY. As Fitzsimons (1995) and Schreiner et al. (1995) both noted, egg density was inversely related to the area of a spawning reef and most man-

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Fig. 2. A comparison of lake trout egg abundance (eggs per 1000 trap days; mean and range) at artificial and natural spawning areas Lakes Superior, Michigan, and Huron using egg traps. Number of individual sites used to calculate the mean is shown beside the range bar. Data are from Marsden (1994) and Schreiner et al. (1995).

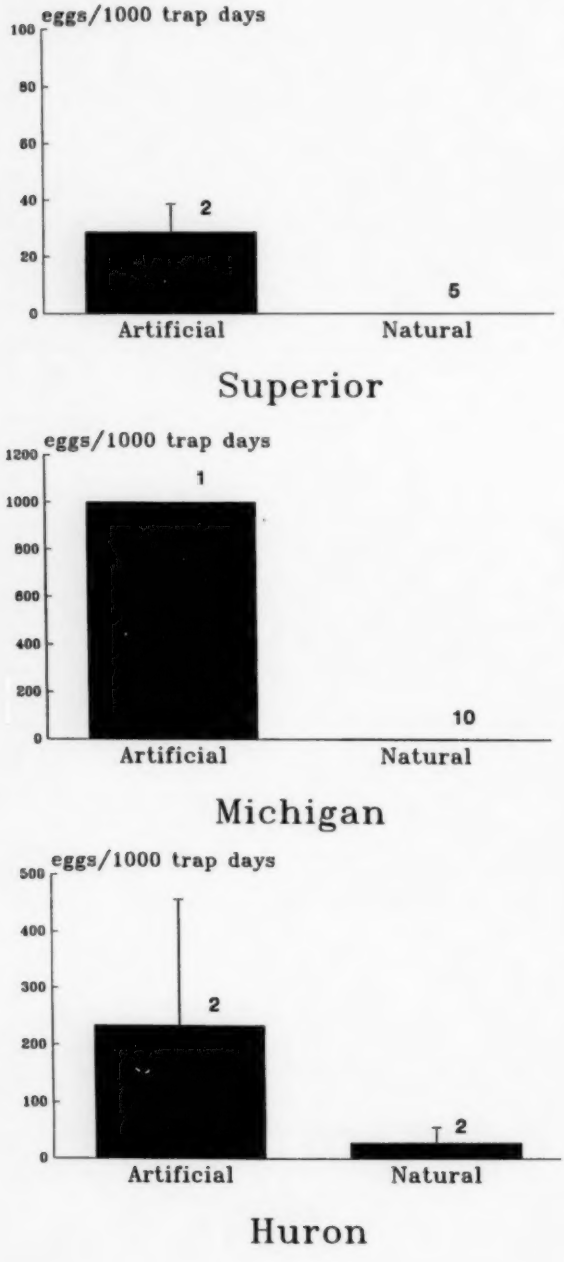
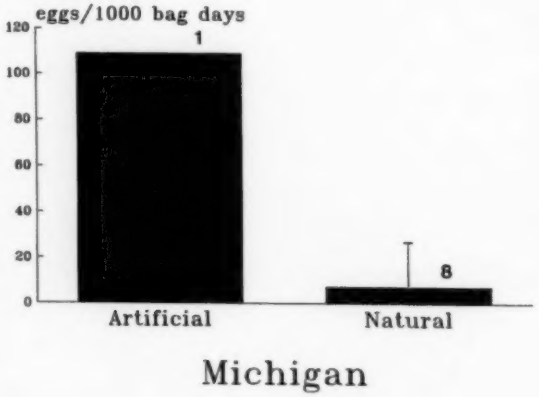


Fig. 3. A comparison of lake trout egg abundance (eggs per 1000 bag days; mean and range) at artificial and natural spawning areas in Lake Michigan using egg bags. Number of individual sites used to calculate the mean is shown beside the range bar. Data are from Marsden (1994).



made structures tended to be smaller than natural spawning areas. When combined with the tendency of lake trout to spawn near shore (Marsden 1994; Fitzsimons 1995; Hansen et al. 1995; Schreiner et al. 1995) and in relatively shallow water (Marsden 1994), high densities of spawning fish are likely to occur in the nearshore areas where man-made structures are located as was documented by Marsden and Krueger (1991) and Fitzsimons (1995). Furthermore, limited habitat availability in the nearshore zone as exists in areas of the Great Lakes (Sly and Thomas 1974) may result in increased spawning on available habitat, namely man-made structures. While substrate size does not appear unique at man-made structures the amount and deep interstices of substrate and relief above the lake bottom may be important. These features combined with the uniqueness of man-made structures in an otherwise featureless environment may serve to attract fish. Their shape may also have the effect of altering currents either by changing direction or speed and these changes could attract spawning fish (Grove and Sonu 1985).

A comparison of the physical characteristics of man-made structures and natural spawning areas used in the Great Lakes

Man-made structures used for spawning by lake trout in the Great Lakes include breakwalls, piers, industrial water intake and discharge overburden structures, and artificial reefs. The area of these man-made structures ranged from 6 to 18 000 m^2 and generally tended to be smaller than for natural spawning areas, some of which were in excess of 100 000 m^2 (Fitzsimons 1995; Schreiner et al. 1995). Water depth varied at man-made structures from 1.8 to 12 m but was similar to that reported for natural spawning areas. The size of material spawned on varied greatly from gravel to boulders for the two habitats although there tended to be more variation in substrate size at natural spawning areas than at man-made structures, possibly reflecting their differing origins. Visual observations of natural historic spawning grounds in Lake Huron indicated

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Fig. 4. A comparison of emergent lake trout fry abundance (fry per square metre; mean and range) at artificial and natural spawning areas in Lakes Michigan and Huron based on emergent fry traps. Number of individual sites used to calculate the mean is shown beside the range bar. Data are from Wagner (1981), Nester and Poe (1984), and Anderson (1995).

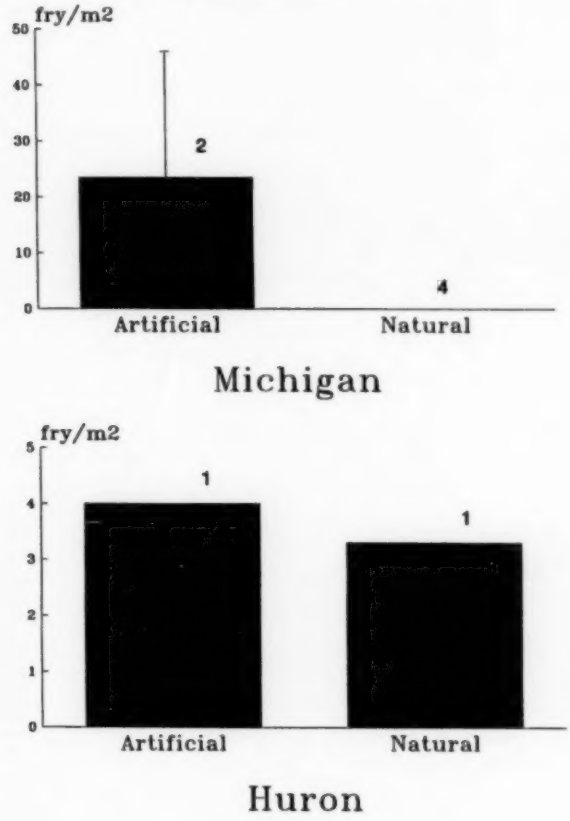
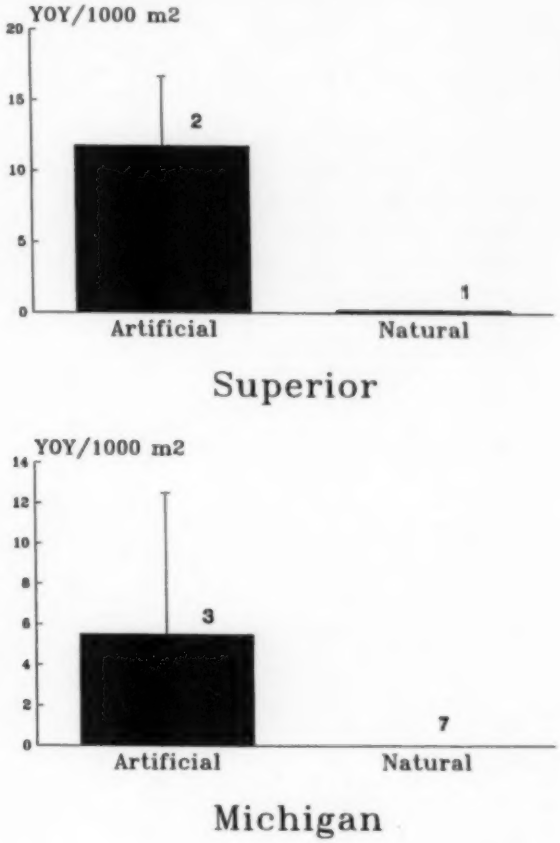


Fig. 5. A comparison of lake trout YOY abundance (YOY per 1000 square metres; mean and range) at artificial and natural spawning areas in Lakes Superior and Michigan. Number of individual sites used to calculate the mean is shown beside the range bar. Data are from Bronte et al. (1981), Jude et al. (1981), Peck (1982, 1986), and Wagner (1981).



that substrate size at these areas was much less homogeneous than at one man-made structure examined (Nester and Poe 1987). The natural spawning areas examined by these authors appeared to be the result of glacial activity but also reflected variable amounts of modern local inputs. Similarly, Kelso et al (1995) reported considerably more variation in substrate size at five natural spawning areas in Lake Superior than was noted by Peck (1986) for a man-made structure in this same lake. Wagner (1981) also reported considerably more variation in substrate size for five natural spawning areas in Lake Michigan than for three man-made structures in this same lake. In contrast, Fitzsimons (1995) found similar amounts of variation in substrate size between two man-made structures and five natural spawning areas in Lake Ontario. Four of the five natural spawning areas Fitzsimons (1995) studied appeared to be relict ice-push features formed during a premodern low water stage in the lake (Sly and Thomas 1974; Sly 1988) while a fifth was a modern cobble gravel beach (Sly and Schneider 1984).

Substrate depth appeared to be greater for man-made structures than for natural spawning areas and likely reflects the different origins for materials found in these two types of habitats. With natural spawning areas that are the result of glacial activity, ice scour and wave activity have, over geologic time, tended to reduce their depth. In contrast, man-made structures being constructed to position material in a confined area have much greater relief and generally steeper slopes than natural spawning areas (Fitzsimons 1995). Depth of substrate at two piers, Burlington Pier and Port Weller, used for spawning by lake trout in Lake Ontario was estimated to be 4–5 m based on the height of material deposited (Fitzsimons 1995; unpublished data). In contrast, depths of five natural spawning areas evaluated by the same author were considerably less (< 2 m) based on their relief above the adjacent lake bottom and diver observations. In Lake Huron, substrate depth at two natural spawning areas, the Tawas reef and Rockport Harbour breakwall, were 2.5 and 1 m thick, respectively (N. Foster, National Biological Service, Ann Arbor, Mich., personal communication; Nester and Poe 1987). These values were considerably greater than values reported by Nester and Poe (1987)

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for 11 natural spawning areas, whose thickness ranged from 0.3 to 0.5 m. Similarly, in Lake Michigan the substrate depths for two breakwalls and a rock crib, reported by Wagner (1981), ranged from 1 to 3.5 m thick while substrate depth at another breakwall studied by Marsden (1994) was 2 m thick. By comparison the substrate depths at eight natural spawning areas studied by Wagner (1981) and seven natural spawning areas studied by Marsden (1994) were substantially less (< 1 m) based on the physical descriptions provided. The average substrate depth of a water intake used for spawning in Lake Superior was at least 2 m (Peck 1986) and much deeper than the 0.2- to 1.5-m depth found at five natural spawning areas in this same lake (Kelso et al. 1995).

Evaluation of characteristics important to the use of man-made structures and artificial reefs for spawning by lake trout

Given the apparently high spawning activity associated with some man-made structures in the Great Lakes, it is of interest to examine some of the factors that could either enhance or detract from their use by spawning lake trout in future. In Lake Michigan, where nine man-made structures have been evaluated, lake trout were found at only five man-made structures with evidence of spawning at only three of these sites (see Jude et al. 1981; Wagner 1981; D'Itri 1985). It is not possible to suggest why some of these structures were used for spawning and some were not. In addition to those sites where spawning did occur, structures were very diverse and included a water intake (Jude et al. 1981), a breakwall (Wagner 1981), and a rock crib (Wagner 1981) ranging in area from 25 to 10 000 m^2. Substrate size, while variable, included areas of 5–30 cm cobble and water depths ranged from 3.5 to 11 m for the three structures that were all associated with the shoreline.

Just as for man-made structures, information available on the use of artificial reefs by spawning lake trout has provided little quantitative information that would be useful for constructing artificial reefs for this species. A total of six artificial reefs have been built in the Great Lakes to enhance fish spawning although two nearshore reefs in southern Lake Michigan, the Hamilton Reef at Muskegon, Mich. (Kevern et al. 1985), and the south shore reef at Milwaukee, Wis. (Binkowski 1985), and an artificial offshore reef in western Lake Ontario (Gannon 1985) were not used by spawning lake trout. Little natural spawning habitat exists in the areas where these three reefs were constructed (Sly and Thomas 1974; Thibodeau and Kelso 1990). In contrast, artificial reefs in Lakes Superior and Huron (Fitgers reef and Tawas reef, respectively) had some of the highest egg abundances observed in these two lakes (Schreiner et al. 1995). Both of these reefs were located in protected areas and close to shore. Alternative natural spawning habitat was relatively scarce based on the locations of historical spawning reefs in the area (Thibodeau and Kelso 1990). Reefs were constructed of cobble substrate in water depths ranging from 3 to 10 m and were steep sided, up to 45°. These reefs were relatively small, ranging in size from < 1000 to 2070 m^2. Spawning by lake trout on these reef structures occurred within 2 years of construction, so it is unlikely that the absence of spawning at the other artificial reefs was due to a failure by spawning fish to locate them.

A sixth artificial reef complex constructed in eastern Lake Ontario provided the only opportunity to quantitatively evaluate the functioning of artificial reefs relative to an adjacent natural spawning area. This complex consisted of six artificial reefs built adjacent to and with the same substrate as a natural spawning shoal at Stony Island (Marsden et al. 1995*b*). Despite their individual sizes (16 m^2), which were 30 times smaller than the adjacent natural spawning area (Perkins and Krueger 1995) and should have favoured their use, egg densities on the artificial reefs were one half to one quarter of those on the natural reef. Egg deposition on the artificial reefs may well have been lower still as eggs may have drifted from the natural spawning area during storms (Perkins and Krueger 1994*a*). The lower egg density on the smaller artificial reefs was in contrast to observations by others (Schreiner et al. 1995; Fitzsimons 1995) that indicated that egg density was inversely related to the size of the spawning area. Some characteristic of the existing natural spawning habitat at Stony Island may be responsible for this difference since this reef has unusually high egg densities relative to other natural spawning areas in Lake Ontario (Fitzsimons 1995). One such characteristic may be imprinting by adults to the abundant lake trout fry and associated fecal and metabolic products at this reef (Foster 1985; Perkins and Krueger 1995). This, however, does not appear to be an absolute requirement as stocked lake trout will spawn in inland lakes that were formerly devoid of the species and where fecal and metabolic products from fry would have been absent (Olver and Lewis 1977; Purych 1980; Hitchins and Samis 1986). While the available studies provide little useful information for constructing artificial reefs, what work has been done indicates that low use is unrelated to the presence of competing natural spawning habitat, the absence of odour substances, abundance of spawning fish, or a failure of these same spawning fish to become aware of a reef's presence.

Design considerations for building artificial reefs

Despite the lack of information on important attributes that will lead to spawning on artificial reefs, important characteristics are evident based on man-made and natural spawning areas. Exposure to currents seems most important as excessive sedimentation and infilling of interstices results in reduced spawning as was noted by Wagner (1981) at Elmwood Harbour. Conversely, excessive exposure to currents can result in almost total egg mortality, as has been observed at a breakwall at Bluffers Park (G. MacPherson, Metropolitan Toronto Region Conservation Authority, Toronto, Ont., personal communication) and a pier at Wellington (J. Fitzsimons, unpublished data), both in Lake Ontario. The effect of exposure appears to be mediated through wind-generated turbulence (Fitzsimons 1995), and its effect on increased shock sensitivity of embryos during early stages of development (Fitzsimons 1994*b*). Although spawning depth appears to be related to lake area (Fitzsimons 1994*a*), building structures at greater depths that are used for spawning may obviate some of the effects of fetch. Given that construction of man-made structures is, in most instances, for purposes other than for use by fish, long fetches may be unavoidable and this may result in high egg mortality.

The tendency of lake trout to move inshore and travel along shorelines prior to spawning would dictate building structures

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adjacent to the shore; however, this may result in high egg mortality due to physical shock as noted above and subject swim-up stage larvae to high levels of predation, most notably by alewife (Krueger et al. 1995; Johnson and VanAmberg 1995).

Depth of substrate and associated depth of interstices at man-made structures tended to be greater than at natural spawning areas and would have the effect of enhancing survival by protecting eggs from washout by waves and currents. Entrapment of eggs within the interstitial spaces would seem to be maximized by using material of the correct size and shape. The ideal substrate size appears to range from 10 to 20 cm and is angular to subangular in shape (Fitzsimons 1995; Marsden and Krueger 1991). Material smaller than this with its accompanying reduced porosity may result in the irreversible accumulation of sediment and organic material that can lead to poor water quality and low egg survival (Garside 1959; Sly 1988; Fitzsimons 1989). Conversely, material that is too large would provide little protection from washout by currents and allow increased access by large-bodied predators (Fitzsimons 1990).

There appears to be a need for a steep drop-off although this requirement is still not fully understood and this would require reefs to be a minimum height. A drop-off may tend to aggregate fish through the effects of a sudden change in depth and its effect on current direction and speed (D'Itri 1985). A reef height of at least 1 m seems necessary although a greater height would seem to enhance a reef's effectiveness not only in influencing currents but also as a visual stimulus for spawning fish. In addition, a greater distance between the top of a reef and the bottom would seem to provide a greater area for entrainment of eggs on the slope itself. Eggs that are moved off the top of a reef by currents and not entrained down its slope may be deposited on unsuitable substrate at the bottom of the reef (Marsden and Krueger 1991; J. Fitzsimons, unpublished observations).

As fish will spawn on a range of sizes of man-made structures reef area does not seem important. Configuration may be more important and reefs should be more elongate than square if possible. At Burlington Pier most spawning was associated with the top of the reef and within 2 m back from the drop-off. Hence, a width greater than 4 m, in the case of a water intake structure for example, may be unnecessary and may result in sediment accumulation in the center of the reef. Side-scanning sonar records of underwater ridges used for spawning in western Lake Ontario (Fitzsimons 1995), indicated increased sedimentation on the tops of these ridges away from the edge of the drop-off (G. Brown, University of Toronto, Toronto, Ont., personal communication).

In summary, artificial reefs should be located close to shore in areas with sufficient but not excessive currents. They should be constructed of 10–20 cm cobble with the depth of interstices of at least 1 m but preferably greater and with a maximum width at the top of the reef of 4 m and a slope from 30 to 45°.

Recommendations

There is a need to increase the availability of spawning habitat for lake trout in parts of the Great Lakes where habitat has been lost. Spawning habitat has been lost in areas like western Lake Ontario (Whillans 1979), and here artificial reefs may make a significant contribution to successful reproduction. However, the quantity and quality of spawning habitat in the Great Lakes is largely unchanged from that existing historically (Marsden et al. 1995*a*). Genetic strains now extant in the Great Lakes as well as those used for stocking, fish-stocking practices, and liberal commercial fishing regulations impose additional constraints on habitat use and to re-establishing self-sustaining populations. Man-made structures, including artificial reefs, may increase spawning habitat. Lake trout egg abundance at most man-made structures was higher than egg abundance at most natural spawning areas. Given their small size and low egg survival in more exposed locations, though, the contribution by man-made structures to lake trout recruitment may be low. Moreover, the reasons for why some structures are used and some are not are not clear. Therefore, I recommend that construction of artificial reefs or man-made structures be approached on an experimental basis to more fully assess their contribution to natural reproduction in the Great Lakes. Such an approach could involve the deliberate creation of artificial reefs or the use of incidental spawning habitat created through the construction of breakwalls, marinas, bridges, piers, and water intake and discharge structures. Technology for creation of spawning habitat is still at the experimental stage and much remains to be learned about factors affecting spawning use and egg and fry survival. Accordingly the construction of artificial reefs to mitigate the loss of existing spawning habitat does not have a well-developed scientific rationale and hence should be avoided.

Construction of artificial reefs should be viewed as part of a strategy to increase access to spawning habitat for lake trout in the Great Lakes. This strategy would include other measures available to fisheries managers, such as stocking, that would make greater use of the existing and abundant spawning habitat that exists.

Presently lake trout in the Great Lakes may be stocked in areas where they did not spawn historically (Thibodeau and Kelso 1990) or where there is little natural spawning habitat (Sly and Thomas 1974), in part to avoid conflicts with commercial fisheries (Hansen et al. 1995). Large areas of apparently good spawning habitat, however, exist in each of the Great Lakes. Stocking of lake trout in these areas, bearing in mind their restricted home range (Ihssen et al. 1988), could improve recruitment more than constructing artificial reefs in areas where habitat is scarce. Restoration of lake trout stocks in the Minnesota and Michigan waters of Lake Superior where there is abundant shoreline spawning habitat succeeded largely on the basis of stocking (Hansen et al. 1995). Conversely, in Wisconsin waters of Lake Superior where nearshore habitat is scarce but offshore habitat is abundant, stocking was not successful in restoring stocks (Krueger et al. 1986). Hence, there is a need for studies to determine how stage at stocking (e.g., eggs, fry, yearlings), proximity to spawning habitats, and stock origin affect population success.

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Importance of habitat and migration to sturgeons with emphasis on lake sturgeon

Nancy A. Auer

Abstract: Sturgeons utilize a variety of habitat types throughout their life: rivers for spawning; rivers, lakes, estuaries, or the sea for feeding and wintering adults; and estuarine areas for feeding young. Distances covered by some sturgeons during spawning migrations show a positive relationship to average adult size. The lake sturgeon, *Acipenser fulvescens*, is the only sturgeon endemic to the Great Lakes basin. Most remaining populations in the basin are restricted in movement, yet a few, free-ranging populations still remain. Study of these populations will more adequately define range and habitat preferences of the species. Some state and federal agencies are now creating management plans for lake sturgeon. Those plans need to be based on information gathered from free-ranging groups. A barrier-free 250–300 km combined river and lake range is suggested as a minimum distance to support self-sustaining populations and distances of 750–1000 km should not be considered unusual. Fishery managers should give barrier removal or fish passage greater consideration than habitat enhancement for populations currently isolated and restricted in range.

Résumé : Les esturgeons utilisent des habitats variés tout au long de leur vie: des cours d'eau pour le frai, des cours d'eau, des lacs, des estuaires ou la mer pour l'alimentation et l'hivernage des adultes et des estuaires pour l'alimentation des jeunes. La distance parcourue par certains esturgeons pendant les migrations de frai présente une relation positive avec la taille moyenne à l'âge adulte. L'esturgeon jaune est le seul qui soit indigène au bassin des Grands Lacs. La plupart des populations qui y survivent encore voient leurs déplacements limités, mais il demeure quelques populations à libres déplacements. L'étude de ces populations permettra de bien définir l'aire de répartition et les habitats préférés de l'espace. Certains organismes d'États ou du gouvernement fédéral élaborent actuellement des plans de gestion pour l'esturgeon jaune. Ces plans doivent reposer sur les données obtenues à partir de groupes à déplacements libres. On propose des zones de cours d'eau et de lacs libres d'obstacles infranchissables sur une distance de 250 à 300 km comme minimum pour la survie de populations auto-suffisantes, mais des distances de 750 à 1000 km ne doivent pas être jugées comme anormalement grandes. Les gestionnaires des pêches devraient accorder une attention plus grande à l'élimination des obstacles ou à la mise en place de passages pour poissons qu'à l'amélioration de l'habitat lors de la mise en valeur de populations actuellement isolées et dont l'aire est limitée.
[Traduit par la Rédaction]

Introduction

Of the 27 species of sturgeons recognized worldwide, most are currently viewed as extinct, endangered, or threatened (Birstein 1993). All sturgeon species have experienced drastic declines in abundance caused by overharvest, barriers to migration, and (or) disturbance or pollution of habitat (Rochard et al. 1990). Fishery closures have not effected increases in abundance of sturgeons as is often the case for other species of fish that mature at earlier ages. Loss of spawning and nursery habitat, coupled with blockage of migratory spawning routes, may be the greatest factors that keep most sturgeon populations repressed. Sturgeons are beginning to gain the attention of state, provincial, national, and international agencies (Houston 1987; Rochard et al. 1990; Birstein 1993), and efforts to protect, reintroduce, or enhance habitat for sturgeon populations are just beginning to grow (Wallace 1991; Graham 1992; Booker et al. 1993; Moreau and Parrish 1994).

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All species of sturgeon have shown drastic declines in abundance; most species are believed to be in some jeopardy of long-term survival if they are not already extinct in the wild (Birstein 1993). The general life history of sturgeons (slow growing, late maturing, intermittent spawning) complicates protection and recovery programs. In some locations, some species such as European Atlantic sturgeon, *Acipenser sturio*, are maintained solely through stocking (P. Bronzi, ENEL Centro Ricerca Termica e Nucleare, Via Monfalcone 15, Milan, Italy 20132, personal communication). Artificial rearing techniques are developed, and stocking is economical for only a few species or hybrids (Conte et al.1988; Steffens et al. 1990). In many areas populations of sturgeons are now restricted in movement because of human activity. Isolated populations are more vulnerable to extinction caused by disease, catastrophic events, genetic isolation, and density-dependent responses (Shaffer 1981; Gilpin 1987). Rehabilitation plans for sturgeons are being based on information gathered from isolated populations and may not give a true picture of life-history requirements of these unique fish. Efforts to conserve sturgeons must include a knowledge of minimum viable population (MVP) size and range needs (Soule 1987).

Although nine species of sturgeon are found in North America only the lake sturgeon, *A. fulvescens*, is endemic to the entire Great Lakes basin. This species is now considered

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Table 1. Summary of ecosystem use by *Acipenser* species worldwide.

Species	Common name	Ecosytem use		
		Freshwater	Estuarine	Marine
Acipenser baeri	Siberian	Votinov and Kas'yanov 1978	Ruban and Konoplya 1994	
A. baeri baicalensis	Baikal	Birstein 1993		
A. brevirostrum	Shortnose	Buckley and Kynard 1985	Hall et al. 1991	
A. dabryanus	Yangtze	Rochard et al. 1990		
A. fulvescens	Lake	Harkness and Dymond 1961		
A. gueldenstaedti	Russian	Raspopov and Putilina 1989		Levin 1992
A. medirostris	Green	Birstein 1993	M.L. Krykhtin and V.G. Svirskii, personal communication[a]	M.L. Krykhtin and V.G. Svirskii, personal communication[a]
A. mikadoi	Sakhalin	Birstein 1993		Birstein 1993
A. naccarii	Adriatic	Birstein 1993	Rochard et al. 1990	Birstein 1993
A. nudiventris	Ship/Sheap	Markarova et al. 1991		Markarova et al. 1991
A. oxyrhynchus desotoi	Gulf	Mason and Clugston 1993	Mason and Clugston 1993	Wooley and Crateau 1985
A. o. oxyrhynchus	Atlantic	Kieffer and Kynard 1993	Kieffer and Kynard 1993	Kieffer and Kynard 1993
A. persicus	Persian	Igumnova and Dubynin 1991		Birstein 1993
A. ruthenus	Sterlet	Tsyplakov 1978	Rochard et al. 1990	
A. schrencki	Amur	Rochard et al. 1990	Rochard et al. 1990	
A. sinensis	Chinese	Q. Wei, personal communication[b]		Q. Wei, personal communication[b]
A. stellatus	Stellate, Sevryuga	Veshchev and Novikova 1983		Trusov 1975
A. sturio	Atlantic (Baltic)	Rochard et al. 1990		Rochard et al. 1990
A. transmontanus	White	Lane 1991	Lane 1991; Kohlhorst 1979	Brown et al. 1992

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[b]Wei, Q., Chinese Academy of Sciences, Yangtze River Fish Research Institute, Shashi, 434000 Hubei, People's Republic of China.

threatened, endangered, or a species of special concern in most of this region (Johnson 1987). This review emphasizes that body size – range relationships exist for sturgeons as they do for other organisms, that range needs must be taken into consideration when developing management plans for these fishes, that a variety of habitats are necessary throughout the life cycle of lake sturgeon, and that recovery efforts for lake sturgeon in the Great Lakes must address restoration of migration routes and protection of habitat for this species. A minimum, unobstructed range for MVPs of lake sturgeon is suggested and habitat access is stressed over habitat enhancement for assuring the future for this species.

Importance of migration to the Acipenseridae

Sturgeons are separated into 4 genera in the family Acipenseridae: *Huso* with 2 species, *Acipenser* with 19 species, *Scaphirhynchus* with 3 species, and *Pseudoscaphirhynchus* with 3 species (Birstein 1993). All migrate in freshwater rivers to spawn, spawn in fast-flowing water, and are slow-growing, late-maturing fishes. Sturgeons may take 10–20 yr to reach maturity and then spawn intermittently.

Fish migrate to optimize feeding, avoid unfavorable conditions, and (or) to optimize reproductive success (Northcote 1978; Tsyplakov 1978; McKeown 1984). Sturgeon may return to historic spawning grounds, but this has only been documented for a few species (Dadswell 1979; Lyons and Kempinger 1992). Homing behavior in fish is thought to facilitate development of population-specific adaptations to the habitat occupied (Leggett 1977). Such behavior is also thought to result in reproductive isolation producing fish stocks unique in behavior, energetics, and reproductive characteristics (Leggett 1977). Three species of sturgeon were known to utilize different areas of the Volga River (Russia) for spawning prior to its impoundment to provide power (Khoroshko 1972). Nikolsky (1963) found that the resistance of egg membranes to rupture under pressure varied among these species. The largest sturgeon in the system, the beluga, *Huso huso*, has the most resistant eggs and spawned furthest upstream, followed by the Russian sturgeon, *A. gueldenstaedti*, which spawned lower downstream, and finally by the stellate sturgeon or sevryuga, *A. stellatus*, which has eggs with the least resistance and spawned lowest in the river system. Such adaptations may optimize survival of eggs in environments of differing harshness.

Blockage of migratory routes may force more than one species to utilize a similar habitat for spawning and hybridization may occur. The three sturgeons that once spawned throughout 2500 km of the Volga River are now confined to 430 km below the Volgograd Dam (Yelizarov 1968). In the United States, the natural ranges of the pallid, *Scaphirhynchus albus*, and shovelnose sturgeons, *S. platorynchus*, overlap; however, locks, dams, and impoundments on the Mississippi River have trapped these species. Where they now occur in close proximity, hybrids are confusing study of the life history of these endangered species (Carlson et al. 1985). Studies with salmonids have revealed that land-locked populations do not fare as well as migratory groups. Migratory forms tend to be more abundant, larger, and more fecund (Northcote 1978;

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Jonsson 1985; Crisp 1994). Whether such characteristics occur in migratory populations of sturgeons has yet to be investigated and may be critical to management for these fishes.

Sturgeons exhibit three general patterns in habitat selection and migratory strategy. Some outmigrate to brackish or estuarine environments after spawning and juveniles follow later; some outmigrate to the sea immediately, young and juveniles as well; and a few species remain in freshwater their entire lives (Rochard et al. 1990). Data on habitat selection and migratory strategy were examined for 19 species of *Acipenser* (Table 1). Only three *Acipenser* species are known to live exclusively in freshwater: the Baikal sturgeon, *A. baeri baicalensis* (a subspecies of the Siberian sturgeon *A. baeri*), which lives in Lake Baikal and spawns in the tributaries of that system; *A. dabryanus,* the Yangtze sturgeon, found in the lower Yangtze River, China; and the lake sturgeon known from the Great Lakes, Hudson Bay, and Mississippi River drainages. The Yangtze sturgeon is considered endangered and close to extinction (Doroshov and Binkowski 1985); natural movement patterns remain unknown, and it is possible that this species utilizes estuarine or ocean environments.

Artyukhin (1995) recently examined the phylogenetic relationships within *Acipenser*. He grouped Siberian sturgeon, shortnose sturgeon, *A. brevirostrum*, and lake sturgeon together in a subgenus based on morphological similarities but also because Siberian sturgeon and lake sturgeon occupy freshwater habitats and the coldest geographic ranges. Siberian sturgeon are found throughout the major river systems of Siberia.

Habitat selection and stage in life cycle

Throughout its life, a sturgeon may utilize several distinct habitats. Different types of habitat are required for the development of eggs and larvae, the growth of juveniles, the feeding and wintering of adults, and spawning by adults.

Larvae

Upon hatching, larval lake sturgeon remain burrowed in gravel until the yolk is absorbed (Kempinger 1988). After most yolk is absorbed young lake, Russian, and sevryuga sturgeon begin to drift downstream (Veshchev and Novikova 1983; Kempinger 1988; LaHaye et al. 1992; Levin 1992; Kurz 1993). Little is known about duration and extent of this drift. Habitat selected by burrowing, feeding, and resting larvae needs to be described.

Juvenile

Perhaps the largest gap in life-history knowledge of sturgeons is defining habitat preferred by young and growing individuals. Some investigation has shown that juvenile Russian sturgeon prefer substrates of fine sediment (Levin 1982), and limited work has been done on movements of juvenile lake sturgeon in a confined system (Thuemler 1988).

Adult spawning

Adult sturgeons usually spawn during the spring in fast-flowing water or main-channel environments, often in the upper reaches of large river systems (Khoroshko 1972; Dadswell 1979; Markarova et al. 1991; Lyons and Kempinger 1992; Parsley et al. 1993). The fish are believed to return to natal areas to spawn and fidelity to such streams is high. Lyons and Kempinger (1992) found that only 3 of 203 lake sturgeon (1.5%) tagged during spawning in the Wolf River, Wisconsin, moved to another river to spawn in a subsequent year. Lake sturgeon may also spawn on wave-washed rocky shorelines of lakes, but documentation of this is historic and incomplete (Smith and Snell 1889; Harkness and Dymond 1961; Carlson 1995).

Adult feeding and wintering

Generalizations concerning feeding and wintering of sturgeons cannot be made because of the various migratory strategies evolved. Some species remain within freshwater-estuarine systems their entire lives and inhabit discrete areas during winter (shortnose sturgeon). Other species outmigrate to the sea and little is known of their movements or habitat preferences (green sturgeon, *A. medirostris*; Atlantic sturgeon, *A. oxyrhynchus*; European Atlantic sturgeon). Some species are restricted in movement or are currently known only from greatly perturbed ecosystems (*Pseudoscaphirhynchus* in the Aral Sea area and *Scaphirhynchus* in the Mississippi and Missouri River systems). Natural range and habitat preferences of such species may never be known. Life history and population assessment is poorly understood for other species such as the Yangtze, Sakhalin (*A. mikadoi*), Adriatic (*A. naccari*), Persian (*A. persicus*), and Amur (*A. schrencki*) sturgeons.

Relationship of body size to range

To protect and eventually enhance populations of sturgeons there is a need to determine species-specific MVP size and range (Gilpin and Soule 1986). The concept of MVP has been applied to terrestrial organisms but rarely fishes. A species' body size – geographic range relationship is important in estimating an abundance for MVP (Soule 1987). Although not often applied to fishes, in other organisms the relationship between body size and range is usually positive (Gaston 1990). McAllister et al. (1986) showed a positive relationship between body size and range for several fish species combined, and Peters (1983) noted a positive relationship between body size as mass (kilograms) and migration distance for birds, mammals, walking insects, and fish (salmon). Schaffer and Elson (1975) also found a positive correlation between mean age at first spawning (body size) and distance of upriver migration for Atlantic salmon, *Salmo salar*.

To determine if a relationship between body size and spawning migration distance exists for sturgeons, I related average body size, average total length of mature fish, and maximum river spawning migration distance (the distance covered in the river by the majority of fishes in a population that uses that river for spawning) using data from the literature (Tables 2 and 3). Body size does not include weight as few studies provided such data. River distances were determined from locations reported in the literature having verified historic or current spawning areas for sturgeons (Table 3).

A simple regression of average adult body length and maximum river spawning migration distance for eight species of sturgeon resulted in an r^2 of 81.3% ($p < 0.001$) (Fig. 1*a*). Maximum known river spawning migration distances for lake sturgeon appear inconsistent with data presented for similar-sized species, and when lake sturgeon was removed from the

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Table 2. Average adult total length or fork length (FL) and weight of selected sturgeon species.

Species	Common name	Sex	Total length (cm)	Weight (kg)	Source
Acipenser baeri	Siberian		105–137	517	Ruban and Akimova 1993
			115–141	10–21	Ruban and Akimova 1991
A. brevirostrum	Shortnose		75 (FL)	4	O'Herron et al.1993
			78–85		Hall et al. 1991
		Male	47–54		Carlander 1969
		Female	5458		Carlander 1969
		Male	51		Scott and Crossman 1973
		Female	61		Scott and Crossman 1973
			50–72		M. Bain, personal communication[a]
A. fulvescens	Lake	Male	76–135		Carlander 1969
		Female	89–140		Carlander 1969
		Male	80–164		Dumont et al. 1987
		Female	117–140		Dumont et al. 1987
		Male	133.4		Folz and Meyers 1985
		Female	160.3		Folz and Meyers 1985
		Male	134	14	N.A. Auer, unpublished data
		Female	154	26	N.A. Auer, unpublished data
A. nudiventris	Sheap	Male	145	16	Markarova et al. 1991
		Female	159	28	Markarova et al. 1991
A. oxyrhynchus	Atlantic	Male	107–198	25	Lee et al. 1980
		Female	200	34	Lee et al. 1980
		Male	133–204	27-35	M. Bain, personal communication[a]
		Female	180	47-125	M. Bain, personal communication[a]
A. sinensis	Chinese		273	214	Q. Wei, personal communication[b]
A. stellatus	Stellate	Male	135	7	Veshchev 1991
		Female	154	13	Veshchev 1991
			130–150	6–13	Birstein 1993
A. transmontanus	White		80–340		Lee et al. 1980
			163–203		Scott and Crossman 1973
			127–165		Carlander 1969
Huso huso	Beluga	Male	223	86	Raspopov and Putilina 1989
		Female	242	124	Raspopov and Putilina 1989

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regression the r^2 became 92.2% ($p < 0.001$) (Fig. 1*b*). Atlantic sturgeon was not included in the regression analysis because potential river spawning migration distances are only known for populations currently affected by barrier dams. Smaller sturgeon species of the genera *Pseudoscaphirhynchus* and *Scaphirhynchus* live in freshwater river systems and do not outmigrate to lakes or oceans. Although these species may be distributed throughout an entire river system, actual distances covered during spawning are unknown. These smaller species are now mostly restricted in range or occur in perturbed ecosystems.

Lake sturgeon

Lake sturgeon are endemic to the Great Lakes basin and were once abundant in all five Great Lakes and connecting waters. Early reports from U.S. waters of the Great Lakes indicate commercial catch of lake sturgeon ranged from 82 000 kg from Lake Superior to 2.1 million kg from Lake Erie for 1885 (Smith and Snell 1889). These catches eventually dwindled to less than 2300 kg by the early 1920s. After commercial fisheries closed in the mid-1900s, the species did not increase in abundance (Harkness and Dymond 1961), possibly because individuals take 10–20 yr to reach maturity coupled with loss of access to spawning habitat and siltation from forest removal practices in the early 1800s. Hydropower and pulp and paper mill dams, many of which were built in the early 1800s, continue to block major lake sturgeon spawning migration routes.

Many major rivers in the Great Lakes once used by spawning lake sturgeon (Table 4) are blocked by dams, and populations are either blocked from access to spawning grounds (as in New York State; Carlson 1995), are restricted in movement (Menominee River, Wisconsin; Cheboygan and Indian lakes, Michigan), or are extirpated from the system (Cuyahoga River, Ohio). Little information is available on use of rivers in Ontario by spawning lake sturgeon. Houston (1987) gave general data on the status of lake sturgeon in Canada, but detailed evaluation of status of the fish in specific river systems was not presented. Houston noted that lake sturgeon may migrate 176–530 km to find suitable habitat for spawning, but I could not verify these distances by examining the three original sources. The data in Tables 3 and 4 emphasize the gap in

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Table 3. River system and known historic (H) or current (C) maximum migration distance by various sturgeon species within that river.

Species	Common name	River system	Migration distance in river (km)	Source
Acipenser baeri	Siberian	Kolyma	800–1085 (H, C)	Ruban and Akimova 1993
		Indigirka	730–850 (H, C)	Ruban and Akimova 1991
A. brevirostrum	Shortnose	Hudson	105 (C, dam)	M. Bain, personal communication[a]
		St. John's	90 (C)	Dadswell 1979
		Connecticut	130 (C, dam)	Buckley and Kynard 1985
		Savannah	278 (H, C)	Hall et al. 1991
A. fulvescens	Lake	Wolf	201 (C, dam)	Kempinger 1988
		Rainy	50–68 (H, C)	Holzkamm et al. 1988
		Bad	32 (H, C)	Shively and Kmiecik 1989
		Sturgeon	69 (C, dam)	Auer (1996)
		Grasse	12 (C, dam)	Carlson (1995)
		Raquette	31 (C, dam)	Carlson (1995)
A. nudiventris	Ship	Syr-Darya	1800 (H)	I. Zholdasova, personal communication[b]
		Amu-Darya	103–1500 (H)	I. Zholdasova, personal communication[b]
A. oxyrhynchus	Atlantic	Hudson	130-182 (H, C, dam)	M. Bain, personal communication[a]
	Gulf	Apalachicola	182 (C, dam)	Wooley and Crateau 1985
A. sinensis	Chinese	Yangtze	2500–3300 (H)	Q. Wei, personal communication[c]
A. stellatus	Stellate	Volga	600–750 (H)	Veshchev 1991
A. transmontanus	White	Columbia	1300 (H)	North et al. 1993
		Fraser	715 (H)	Lane 1991
Huso huso	Beluga	Volga	2100–2500 (H)	Khoroshko 1972

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Fig. 1. Relationship of average adult total length to river spawning migration distance for (a) eight species of sturgeon and (b) seven species of sturgeon (lake sturgeon data removed).

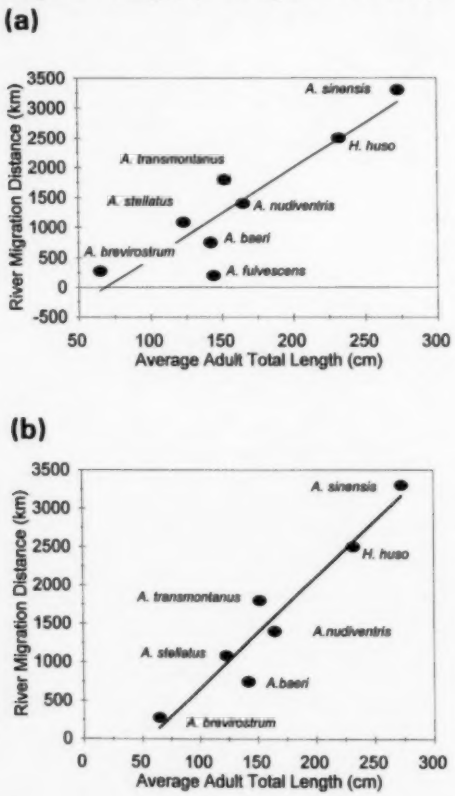
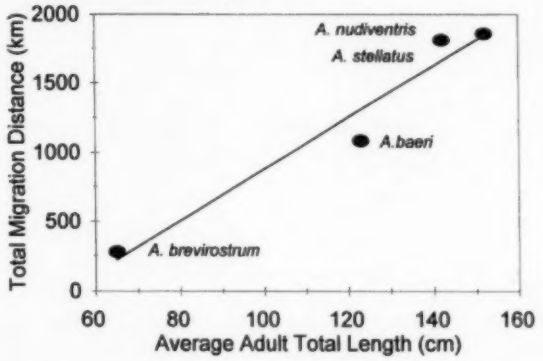


Fig. 2. Relationship of average adult total length to total migration distance for four *Acipenser* species.



knowledge of actual distances required for lake sturgeon spawning migrations.

Because some *Acipenser* species live their lives within freshwater and (or) estuarine environments, total migration distance can be determined for four species (Table 1, Fig. 2). Siberian and shortnose sturgeons live in freshwater rivers and the estuarine areas near the river mouths, so the distance between the river mouth and spawning site would be the maximum possible spawning migration distance, 1085 and 278 km, respectively (Table 1). The sevryuga and Ship (*A. nudiventrus*) sturgeons spawn in freshwater rivers connecting to the Caspian, Azov, and Black Seas (Table 1). If the greatest distance across the Caspian Sea (approximately 1060 km) is added to possible river migration distance (Table 1), the maximum possible migration distance becomes 1811 and 1860 km

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Table 4. Examples of access to and evidence of historic spawning grounds for lake sturgeon in rivers within the Great Lakes basin.

State or province	Lake	River	Blockage	Distance	Source
Minnesota	Superior	St. Louis	Natural falls at Jay Cooke Park	22 km	
Wisconsin	Superior	Bad River	Natural falls	32 km	Shively and Kmiecik 1989
	Michigan	Fox	14 locks and 17 dams	At mouth and throughout	D. Folz, personal communication[a]
	Michigan	Menominee	Upper Scott	At mouth and 4 other sites	Thuemler 1985
	Michigan	Peshtigo	Peshtigo Dam	14 km	FERC 1981
	Michigan	Oconto	Oconto Falls Dam	6 km	FERC 1981
Michigan	Superior	Ontonagon	Victoria Dam	38 km	
	Superior	Sturgeon	Prickett Dam	69 km	Auer 1996
	Michigan	St. Joseph	Berrien Springs Dam	37 km	Baker 1980
	Michigan	Indian Lake and Manistique River	Near lake outlet and on river	2 km below lake outlet and on river	Bassett 1981
	Michigan	Manistee	Tippy Dam	45 km	FERC 1981
	Michigan	Muskegon	Croton Dam	67 km	FERC 1981
	Michigan	Grand	Grand Rapids	64 km	
	Huron	Cheboygan	Cheboygan Dam	At mouth	Hay-Chmielewski 1987
	Huron	Ausable	Foote Dam	14 km above mouth	
	St. Clair	St. Clair	None		
Ohio	Erie	Cuyahoga			Trautman 1981
		Maumee	Independence Dam	77 km	Trautman 1981
		Sandusky			Smith and Snell 1889
New York	Ontario	Black	Dam	1.6 km of mouth	Jolliff and Eckert 1971
		Oswegatchie	Dam	1.6 km of mouth	Jolliff and Eckert 1971
		Grasse	Massena Dam	12 km above mouth	Carlson 1995
		Raquette	Dam	30 km above mouth	Carlson 1995
		St. Regis	Dam	At mouth	Carlson 1995
Ontario	Ontario	Severn Nipigon	Dam	At mouth	
Quebec	St. Lawrence	St. Lawrence	Robert Moses Dam	Created Lake St. Lawrence	Jolliff and Eckert 1971
			Iroquois Dam	28 miles above Robert Moses Dam	Jolliff and Eckert 1971
	St. Lawrence	Rivière Des Prairies and Ottawa River			Fortin et al. 1993
	St. Lawrence	L'Assomption and Ouareau			

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for these species, respectively. When a regression is preformed on the total migration distances and average adult total length for these four species the resulting r^2 value is 95.5% ($p < 0.001$) (Fig. 2).

These data indicate that an average adult lake sturgeon (approximately 144 cm total length) should be capable of migrating distances of 1000–1800 km; however, research to date reveals that this species migrates smaller distances in rivers. In some areas of the Great Lakes, rivers with natural barriers and unaltered by human activity support lake sturgeon populations (Table 4). Lake sturgeon migrate 32 km in the Bad River, Wisconsin, to spawn near natural falls and steep rapids (Shively and Kmiecik 1989). Lake sturgeon in the Grand River, Michigan, meet an impassable set of rapids 64 km upstream, and in the Sturgeon River, Michigan, lake sturgeon migrate 69 km to a set of rapids immediately below a small hydroelectric facility (Auer 1996). Such distances, if considered total migration distances, are much less than migration distances covered by other species of *Acipenser* of similar size (Fig. 2).

In the Lake Winnebago system, Wisconsin, some lake sturgeon were found to travel 228 km to spawn. These fish traveled 201 km within the Wolf River as well as 27 km across Lake Winnebago (Lyons and Kempinger 1992). In the Sturgeon River, Michigan, tagged, postspawning lake sturgeon immediately left the river (69 km) and were recovered at distances of 265 km from the spawning site. Movements of lake sturgeon were studied in the St. Lawrence River by Dumont et al. (1987) and Fortin et al. (1993), who found that these fish move distances of 138–225 km; however, these authors did not determine if these distances were covered during spawning activities.

Discussion

Gonad maturation in fishes often occurs during spawning migrations (McKeown 1984). Females of some sturgeons, when prevented from reaching spawning areas because of barrier dams or manipulated water flows, either resorb eggs and do not spawn or survival of spawned eggs is reduced (Artyukhin

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et al. 1978; Veshchev and Novikova 1983, 1988). In the Wolf River, Wisconsin, lake sturgeon are blocked from upstream migration by the Shawano Dam, and divers report eggs spawned below the dam to be in masses as much as 15 cm thick (Kempinger 1988). Eggs in such masses may show reduced survival, poorer hatch success, and may be more vulnerable to disease and predation. Thick masses of eggs have not been observed on the Sturgeon River, Michigan, where lake sturgeon spawn over a 0.8 km area of rapids (N.A. Auer, unpublished data). Eggs in the Sturgeon River were observed adhering to the underside of clean rock or in rock crevices singly or in very small clusters of 5–20 eggs, but large thick masses of eggs were not observed (N.A. Auer, unpublished).

The sustainability of sturgeons is questionable worldwide (Birstein 1993); exploitation, habitat destruction and pollution, and barriers to migration threaten their future. For a fish that spawns intermittently and can take 10–20 yr to reach maturity, such lost recruitment may prevent the rebuilding of depleted stocks. Data presented in this paper indicate that body size as average adult total length and upriver spawning migration distance are strongly related for eight sturgeon species and that body size as average adult total length and total migration distance are positively related for at least four *Acipenser* species. The lake sturgeon, which has evolved to an exclusive freshwater existence, appears to combine river and lake distances in spawning migrations. These distances may be important for optimum maturation of eggs and sperm prior to spawning and allow for separation of distinct stocks within the Great Lakes.

In the Great Lakes basin, enhancement and management plans for lake sturgeon are only now being developed (i.e., State of Michigan, Lake Sturgeon Management Plan; Great Lakes Fishery Commission, Lake Superior Technical Committee on Lake Sturgeon). These plans are structured after the suggestions of Williams et al. (1988) who presented guidelines for introductions of threatened and endangered species. These authors suggest that introduction sites must meet life-history requirements of the species and contain sufficient habitat to support a viable population. For lake sturgeon, few sites remain for determining what constitutes habitat necessary to support a viable population.

Two river systems in the United States that currently support unrestricted populations of lake sturgeon provide information on optimum habitat characteristics for this species: the Sturgeon River, Michigan, and the Bad River, Wisconsin. First, lake sturgeon spawn in sections of rapids in the upper reaches of each river. Second, there is open access to Lake Superior for feeding and wintering needs. Finally, each river mouth is surrounded by rich organic sloughs that may be necessary for the growth of newly hatched and juvenile individuals. These two systems could be models in protection and recovery efforts. Sites selected for rehabilitation and restocking should allow lake sturgeon access to a minimum of 250–300 km of unrestricted habitat and migratory distances of 750–1000 km should not be considered unusual for this size sturgeon. Retaining open corridors between river and lake environments or providing fish passage must be given priority over enhancement of habitat in isolated environments. For lake sturgeon, opening access to historic spawning areas, allowing for safe outmigration to feeding and wintering areas, and identifying and protecting juvenile habitat will be critical to long-term survival of minimum viable populations in the Great Lakes basin.

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Habitat requirements of northern pike (*Esox lucius*)[1]

John M. Casselman and Cheryl A. Lewis

Abstract: Over the past half century, habitat changes have significantly affected production of northern pike (*Esox lucius*), especially in the Great Lakes Basin. Loss of wetlands, reduction of shoreline cover and structure, cultural eutrophication, and siltation have negatively affected water transparency, abundance of macrophyte habitat, and even body condition. We review recent habitat restoration programs conducted in the Great Lakes Basin to reverse this trend. However, assessment has usually been inadequate to evaluate their success. Spawning and nursery requirements (first year of life) are examined, using a system for classifying and ranking major physical characteristics and requirements. Depth of nursery habitat is directly correlated with fish size and age. Spawning habitat is usually less critical or limiting but more easily manipulated and restored than nursery or juvenile-adult habitats. Year-class strength over 22 yr in eastern Lake Ontario was correlated positively with midsummer temperature and negatively with late summer–early fall water elevation; also, the largest year-class appeared immediately after catastrophic winterkill of a predator, white perch (*Morone americana*). Both implicate nursery rather than spawning associations. Adult abundance is related to the extent of macrophyte cover, which is optimal from 35 to 80% but inversely related to body size.

Résumé : Depuis un demi-siècle, les modifications de l'habitat ont nettement affecté la production de grand brochet (*Esox lucius*), particulièrement dans le bassin des Grands Lacs. La disparition des milieux humides, la réduction du couvert et de la structure des littoraux, l'eutrophisation due à l'agriculture et la sédimentation ont eu des effets négatifs sur la transparence de l'eau, l'abondance de l'habitat des macrophytes, et même la condition corporelle des poissons. Nous examinons des programmes de restauration des habitats qui ont été récemment mis en oeuvre dans le bassin des Grands Lacs pour renverser cette tendance. Les moyens d'évaluation n'ont toutefois pas permis de mesurer le succès de ces programmes. Nous examinons les besoins en frayères et en nourriceries (première année de la vie) à l'aide d'un système de catégorisation et de classement des principales caractéristiques et exigences physiques. La profondeur de l'habitat de nourricerie est directement corrélée à la taille et à l'âge des poissons. L'habitat de fraye est généralement moins critique ou moins limitant, mais plus facile à manipuler et à restaurer que l'habitat de nourricerie ou celui des juvéniles et des adultes. Sur une période de 22 ans, dans l'est du lac Ontario, l'effectif des classes annuelles étaient corrélé positivement à la température au milieu de l'été et négativement à la montée des eaux à la fin de l'été et au début de l'automne; de plus, la classe annuelle la plus nombreuse est apparue après une mortalité catastrophique d'un prédateur, le baret (*Morone americana*). Dans les deux cas, l'association se situerait au niveau des nourriceries plutôt que des frayères. L'abondance des adultes est en rapport avec l'étendue du couvert des macrophytes, qui est optimale dans une proportion de 35 à 80 %, mais en relation inverse avec la taille corporelle.
[Traduit par la Rédaction]

Introduction

Cultural eutrophication and habitat loss over the past half century have significantly affected northern pike (*Esox lucius*) production in North America and especially in the Great Lakes. Northern pike are large keystone piscivores that are important in "top-down" predatory regulation of the fish community. They can tolerate a wide range of environmental conditions but are primarily mesothermal, or cool-water, fish best adapted to shallow (< 12 m), productive, mesotrophic-eutrophic environments. They are a common and abundant species, found in 45% of the total freshwater area of North America (Carlander et al. 1978).

Commercial harvest of northern pike from the Great Lakes declined from a high of 1.6 million kg just after the turn of the century to < 0.05 million kg in the late 1960s (Baldwin et al. 1979). This decline, which was greatest in Lake Erie, followed by Lakes Ontario, Huron, Michigan, and Superior (Fig. 1), was directly proportional across the lakes to the original abundance of the species and the extent of European settlement and associated shoreline alteration. Throughout the period of decline, fish communities were transforming, exacerbated by changes in water levels, temperature, shoreline development, watershed alterations, siltation, aquatic macrophyte cover, commercial and sport fishing, and other factors (Whillans 1979). Changes to nearshore habitats had a particularly impor-

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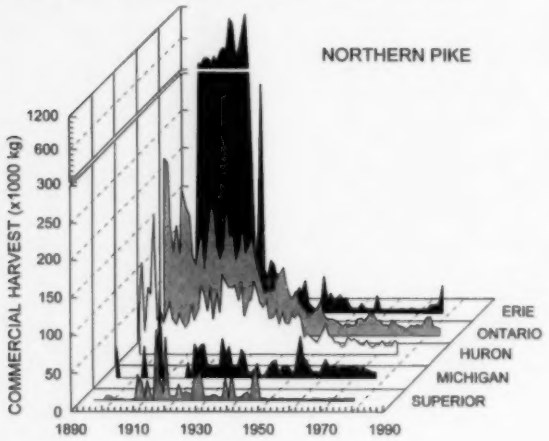
Fig. 1. Commercial harvest of northern pike from the five North American Great Lakes from the early 1900s to the 1970s. Harvest estimates are for the Canadian waters of lakes Ontario, Erie, Huron, and Superior. Data are from Baldwin et al. (1979).



tant negative effect on pike production and have been important in contributing to the decline of the species, reflected in the decrease in commercial harvest (Fig. 1). These changes were most obvious in the more eutrophic lower Great Lakes.

Since settlement on the Canadian shoreline of Lake Ontario, there have been substantial losses of marshes that would have contained spawning and nursery (young-of-the-year) habitat for northern pike. Whillans (1982) concluded that 50% of 62 marshes had been completely lost by the late 1970s. He noted that where populations were densest around the Great Lakes, baseline wetland had been reduced by 75–100%. Most remaining shoreline wetlands on the Great Lakes are degraded and altered by siltation and turbidity and are dominated by silt- and turbidity-tolerant fish species (Jude and Pappas 1992). Dodge and Kavetsky (1994), in their review of aquatic habitat and wetlands of the Great Lakes, concluded that the loss of inshore and nearshore habitat used by northern pike was moderate to low in Lakes Superior and Huron, moderate in Lake Michigan, high in Lake Ontario, and high to very high in Lake Erie. This habitat reduction is directly related to the decrease in commercial harvest of the species throughout the Great Lakes since the turn of the century (Fig. 1). Many recent habitat restoration programs across the Great Lakes explicitly identify the restoration of northern pike habitat as part of the fish community and habitat goals, objectives, and targets (Hartig 1993).

We examine habitat requirements of northern pike throughout its life history by considering spawning, nursery, and juvenile-adult habitat in relation to vegetative cover and substrate, water temperature, oxygen, transparency, and turbidity. Specifically, we (*i*) review the literature, (*ii*) present a system for classifying and ranking habitat associated with spawning and nursery grounds, (*iii*) analyze new data concerning nursery habitat, considering depth distribution and year-class strength for the Bay of Quinte and eastern Lake Ontario for a 22-yr period (1971–1992), and (*iv*) review and evaluate some recent restoration projects.

Habitat requirements of northern pike

Spawning habitat

There are many thorough and practical studies, reviews, and bibliographies of the spawning habitat and requirements of northern pike (e.g., Clark 1950; Johnson 1957; Franklin and Smith 1963; Forney 1968; Coble 1972; McCarraher and Thomas 1972; Alldridge and White 1980; Crossman and Casselman 1987; Raat 1988; Masse et al. 1993). Habitat suitability index models have been developed (Inskip 1982), and those aspects associated with spawning and nursery habitat have been refined and improved (Anderson 1993). Documentation of the loss of spawning habitat is historic and extensive (Brynildson 1958; Threinen et al. 1966, 1969; Reid 1990).

Quite generally, northern pike spawn in shallow water over vegetation in spring shortly after ice-out, when these shallows have warmed to 8–12°C. The fish tend to migrate up tributaries to flooded marshes and wetlands or shallow shoreline inundations. Optimal spawning substrate is flooded vegetation in a shallow, sheltered area. Grasses and sedges are preferred, but other vegetation may be used. The vegetative hummocks and mats should be adequate to entrap the eggs and suspend them above the substrate, where anoxic conditions can develop.

We devised a system for classifying, ranking, and weighting the physical requirements of habitat used by spawning northern pike (Table 1) that uses criteria gleaned from published literature, court evidence (J.M. Casselman, unpublished data), and extensive field observations of spawning northern pike in 18 marshes and wetlands. The system emphasizes the importance of vegetative type, water level, the exposure of a site, its proximity to connecting waterways, and to a lesser extent, substrate type and water exchange (Table 1). We use a simple single-digit ranking system to compare among and within these important habitat variables. Although other attributes could be considered, these physical conditions are of primary importance and are usually readily apparent on site inspection. These criteria apply to spawning time; however, some can be reasonably evaluated at other times of the year (e.g., vegetative type and density). The system can be used to build a matrix to numerically rank and compare and contrast the extent and quality of various habitats.

Spawning success has been linked to water-level changes (see review by Inskip 1982). High water levels at time of spawning with stable levels after the incubation period are associated with large year-classes of northern pike (Johnson 1957). High water levels increase nutrient concentrations and primary and secondary production in inundated areas, increasing the amount of available prey for the larval fish, make more spawning habitat accessible, expand the amount of cover, and reduce the potential for predation and cannibalism. This is obvious when new impoundments are flooded and previously unflooded terrestrial vegetation is inundated. Production of young-of-the-year can be 4–10 times greater the first year after impoundment than in subsequent years (Bodaly and Lysack 1984). Widely fluctuating water levels can inhibit the development of nearshore vegetation; as well, very consistent annual levels are less productive, with low levels being least productive (e.g., Inskip 1982; Gravel and Dubé 1980).

Other environmental conditions can be critical for early life

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Table 1. Criteria for classifying and ranking physical characteristics of spawning and nursery habitat of northern pike using a subjective numerical ranking system that ranges from 1 (lowest, poorest) to 9 (highest, best) and can be used to document and quantitatively describe the relative importance of various habitat characteristics.

Habitat variable	Rank of relative importance	General habitat description: Best (highest rank 9)	General habitat description: Poorest (lowest rank 1)
		Spawning habitat	
Vegetation			
Type	9	Hummocks of grasses and sedges (e.g., *Carex* spp.) meadowgrass *Calamagrostis canadensis*	Cattails, bog laurel, Potamogeton spp., floating aquatic plants
Density	8	Moderately dense, 2–4 hummocks per m^2	Sparser or denser
Water level			
Depth[a]	9	10–70 cm, averaging 20–40 cm (high water associated with strong year-classes)	Deeper or shallower
Fluctuation	7	Gradually increasing prior to spawning; stable until fry start to move from spawning grounds, approximately 6–8 weeks, then gradually decreasing	Fluctuating or not increasing prior to spawning; decreasing abruptly immediately after spawning
Exposure of the site	6	Sheltered, warming rapidly in early spring; receiving direct sunlight from south or west	Warming very slowly in early spring; exposed to north or east
Connecting waterways	4	Rivulets that permit easy movement of spawners into more sheltered spawning areas of the marsh and allow fry to move out with receding water	Few or no deeper connecting channels for drainage or access, or very deep channels congregating predators
Substrate type	3	Well-oxygenated vegetative detritus; good rooting medium for inundated grasses and sedges	Decomposing organic debris or any type of relatively infertile organic or inorganic substrate
Water exchange	2	Moderate; during high water some exposure to wind and wave action	Little or no wind exposure or water movement, or extreme water movement or wave action
		Nursery habitat[b]	
Proximity to spawning habitat	9	Contiguous	More distant or separated from the spawning ground by various obstructions or restrictions, docks, etc.
Vegetation			
Submergent and emergent	8	Dense submergent and emergent aquatic plants (40–90% cover)	Sparser or denser
Extent	6	Extensive; >10 times size of adjacent spawning habitat	Limited; equal in size to adjacent spawning habitat

Note: For simplicity, we defined only extremes. Nursery habitat applies to young northern pike that are older than yolk-sac fry and younger than 1 yr old (young-of-the-year). Depth of nursery habitat is detailed in Figs. 2 and 3. A guideline for determining nursery habitat is that the water is approximately 10 cm deep for every 10 mm of body length (more precisely 12) or for every week after peak spawning.

[a]This criterion describes North American populations because in Lake Windermere, England, pike spawn in 2.0–3.5 m of water over *Elodea*, *Myriophyllum*, and *Nitella* (Frost and Kipling 1967).

[b]The general rule of thumb for locating and determining nursery habitat, detailed above, can be used as a habitat variable. If so, its rank of relative importance is 8, and poorer conditions would involve either much shallower or deeper water.

stages. When oxygen concentration falls below 30–35% air saturation, hatch of northern pike eggs and survival of embryos and larvae are greatly reduced (Siefert et al. 1973). Hydrogen sulphide increases when dissolved oxygen concentrations decrease. Hydrogen sulphide concentrations > 4–6 $\mu g \cdot L^{-1}$ decrease growth and survival of sac fry (Adelman and Smith 1970). Hummocks and vegetative mats are optimal spawning substrate because they help keep the eggs suspended in better oxygenated water, away from anoxic conditions and elevated hydrogen sulphide in the organic sediments.

Northern pike embryos are sensitive to heavy siltation resulting from movement of organic sediment caused by excessive wave action and currents. Siltation of 1.0 $m \cdot day^{-1}$ was associated with mortality exceeding 97% (Hassler 1970).

Nursery habitat

As is true for many species, nursery (young-of-the-year) requirements for northern pike are much less thoroughly studied than spawning habitat requirements. This is partly because young-of-the-year are often solitary, difficult to catch, require specialized sampling techniques or gear (e.g., electrofishing

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Fig. 2. Relations between depth at time of capture and total length and age of young-of-the-year northern pike. Relations between (A) depth and (B) total length are plotted on number of days and date after peak spawning, which during the study period occurred during the last week in April. Northern pike were caught in 1968 to 1971 in two shallow lakes (<3 m), Wickett and Smoky Hollow. Regressions, correlation coefficients, and probability levels are provided.

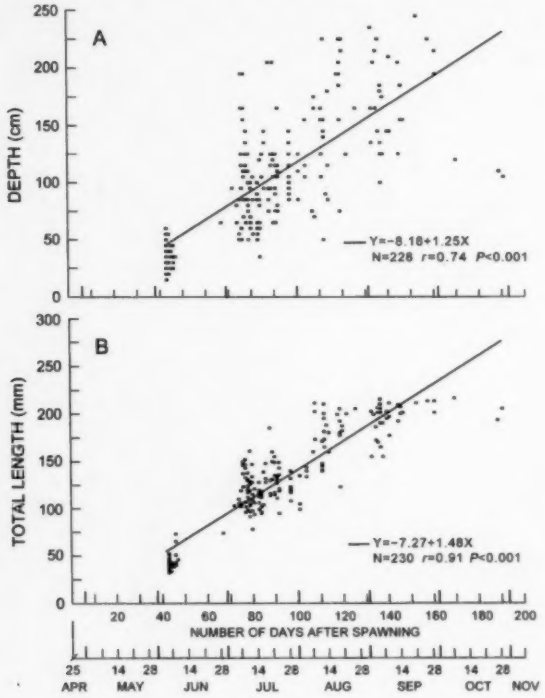
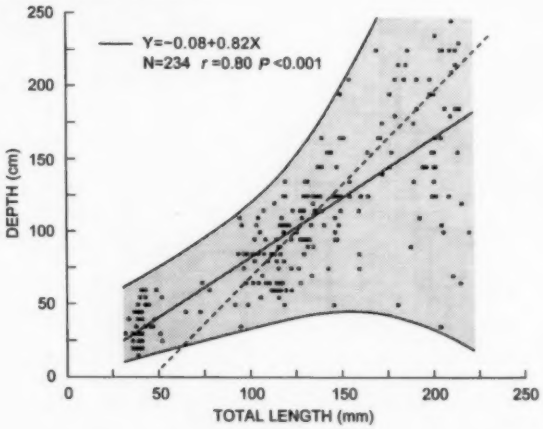


Fig. 3. Relation between depth at which young-of-the-year northern pike were captured throughout the year by electrofishing and Plexiglas traps (Casselman and Harvey 1973) and total length. Regression equation (solid line), correlation coefficient, and probability level are provided. Broken line illustrates the predictive regression of body length on depth. Northern pike were caught from 1968 to 1971 in two shallow (<3 m) lakes, Wickett and Smoky Hollow. Shaded area and lighter curved lines of best fit delineate the extremes.



gear or Plexiglas traps; Casselman and Harvey 1973), and either are caught in low numbers or, if congregating, catches are much more variable when compared with older, larger life stages; this all affects predictability. Activities in the deeper, more extensive nursery habitats are less easily observed than those associated with spawning. It is difficult to study small fish in the natural environment, especially when they are not easily caught or handled. This lack of knowledge has led to the misconception that nursery habitat and requirements are probably less limiting and important than spawning habitat requirements.

Because young fish in the nursery environment grow rapidly and increase in size and activity, their physical habitat needs expand. As they disperse into deeper water, they are usually found in moderately dense vegetation. Presumably, this increased activity makes them more vulnerable to predation, so dense vegetative cover is important in providing them shelter, enhancing survival. Although woody debris and other structures can afford cover and are sometimes important, young northern pike prefer submerged vegetation with some emergent and floating vegetation interspersed. Such cover is especially critical. Johnson (1960) found that growth in tanks devoid of vegetation was erratic and considerably less than when northern pike were reared with vegetation.

The relationships between depth of the habitat, length, and age of young-of-the-year northern pike were examined with electrofishing and Plexiglas trap catches from 1968 to 1971 in two shallow lakes (< 2 m deep) on Manitoulin Island. Sampling effort was distributed uniformly over all depths throughout the open-water period. Depth and age (of young-of-the-year) were highly correlated (Fig. 2A). Since the fish grew during the period, length was linearly correlated with age over the size range studied (Fig. 2B). Hence, the relationship between water depth and size of northern pike during the first year was highly correlated (Fig. 3). This quantified the association between habitat depth and size and age of young northern pike, confirming that as fish grow, their preferred depth range increases. This relationship appears to be less significant in larger, older young-of-the-year; in late summer and early fall, large individuals appear to use a wider range of depths (Fig. 3). These quantitative results make it possible to devise practical criteria for describing depth of young-of-the-year nursery habitat, based on age and date. A general guideline for describing the habitat frequented by young northern pike during the first year is that the water is approximately 10 cm deep for every 10 mm of body length (more precisely 12) or for every week after peak spawning, at least until they reach 150 mm in length.

Anderson (1993) used field surveys and laboratory preference experiments to develop suitability indices for water depth, vegetation type, and density for young northern pike in their nursery habitat. He concluded that intermediate densities of vegetative cover were optimal and that young-of-the-year preferred a combination of submerged and emergent vegetation with densities ranging from 20 to 50%. Predator feeding

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Fig. 4. Proportional year-class strength of northern pike from the Bay of Quinte and eastern Lake Ontario for a 22-yr period from 1971 to 1992.

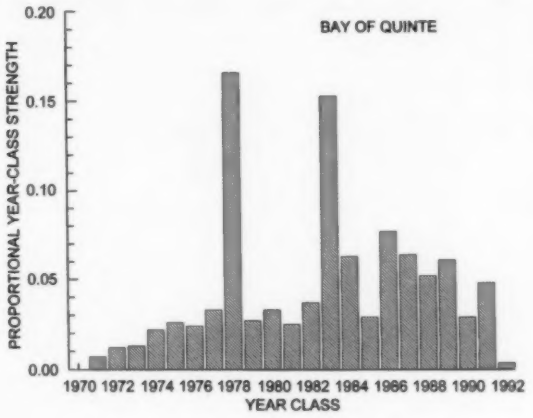

Table 2. Correlation between mean monthly water temperature of the Bay of Quinte for the open-water period (March–December) and the logarithm of the proportional size of the year-class of northern pike from the Bay of Quinte and eastern Lake Ontario from 1971 to 1992.

	Temperature			
Month	Mean	95% CI	r	P
March	1.5	0.34	0.391	ns
April	6.7	0.89	0.226	ns
May	14.7	0.61	0.141	ns
June	20.4	0.48	0.255	ns
July	23.5	0.41	0.569	0.006
August	23.2	0.49	0.540	0.010
September	19.1	0.38	0.182	ns
October	12.2	0.52	0.219	ns
November	5.8	0.54	0.152	ns
December	1.4	0.26	0.497	0.019
March–December	12.8	0.29	0.483	0.023

Note: Daily water temperatures were from the Belleville, Ont., domestic water filtration plant. Probability values are provided. ns, not significant.

efficiency is reduced in areas of dense cover (Cooper and Crowder 1979) and in habitat of increased complexity (Savino and Stein 1982). Anderson (1993) observed that young northern pike preferred *Myriophyllum* and *Potamogeton* over *Scirpus* and *Vallisneria*. Optimal predator efficiency and productivity occurred with intermediate plant densities, where preferred prey could be easily caught but prey populations were not decimated. This was also important for muskellunge (*Esox masquinongy*) (Craig and Black 1986).

Young northern pike in the upper Mississippi River were 10 times more abundant in emergent vegetation and 3 times more abundant in submergent vegetation than in areas that were unvegetated (Holland and Huston 1984). The authors concluded that this preference was related to cover and not to food. Young fish that are associated with deeper and less restrictive habitats grow more rapidly because they are more piscivorous than fish living at confined depths in channels (Mann and Beaumont 1990). In confined marshes and backwaters, the migration of young fish in fall is associated with decreased water temperature and, in some cases, reductions in dissolved oxygen concentration (Holland and Huston 1984; Derksen 1989).

We extended the system for classifying and ranking the physical requirements for spawning habitat to young-of-the-year nurseries (Table 1). We used field observations of young-of-the-year nursery habitats in 12 different lakes in Ontario and data from Anderson (1993). These emphasize the importance of the proximity of quality nursery habitat to spawning habitat and the extent and type of vegetative type and cover, which we estimate to be optimally 40–80%. These physical habitat conditions are most obvious on site inspection; they apply to the summer period, but proximity of habitats can be evaluated at other times of the year.

Optimum temperature for linear body growth of young-of-the-year northern pike was higher (22–23°C) (J.M. Casselman, unpublished data) than that of age 1 and older (19°C) (Casselman 1978) when the same fish were studied. Bevelhimer et al. (1985) observed that maximum growth of young northern pike in Ohio (24–25°C) was higher than that reported by Casselman. They attributed this apparent difference to adaptation resulting from 25 yr of selection in warm Ohio hatchery ponds; however, Bevelhimer et al. studied younger, smaller fish (young-of-the-year, total length (TL) range 125–210 mm, total weight (TW) mean 19.3 g) than did Casselman, who used much older, larger fish (second and third calendar years of life, TL range 281–466 mm, TW mean 340 g). So the results published for these two studies were not exactly comparable. When fish of the same age are compared (young-of-the-year), unpublished results reported above are more similar to those of Bevelhimer et al. (1985) (22–23 vs. 24–25°C); however, a difference exists, although slight, that may be attributed to high temperature adaptation. Fry have an optimum temperature for growth that is even higher (25.6°C; Hokanson et al. 1973). It is apparent that the optimum temperature for growth of northern pike decreases with age.

Small northern pike are more tolerant of oxygen depression than are larger individuals, and critical values are lower (Casselman and Harvey 1975). Casselman (1978) has reported summer mortalities of young-of-the-year resulting from oxygen depression because of prolonged respiration of dense vegetation on dull, calm days.

We examined 22 yr of data on relative year-class strength of 489 northern pike from the Bay of Quinte and eastern Lake Ontario to determine what environmental factors affect recruitment or survival. Fish were collected over a 14-yr period from 1980 to 1994 (fork length (FL) = 66.5 ± 0.9 cm, TW = 2.20 ± 0.10 kg, mean ± 95% CI) in a routine indexing program conducted by Research and Assessment, Ontario Ministry of Natural Resources. Fish were captured in multimesh experimental gill nets and bottom trawls. Similar effort was used each year. Cleithra were used to assess age. Proportional strength of each of the 22 year-classes was measured by calculating the relative abundance of each year-class in each year of sampling, estimating their proportion by age, and averaging this proportion over the ages vulnerable to the sampling gear. The correlations between the mean monthly water temperature

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Fig. 5. Relation between the logarithm of the proportional size of the year-class of northern pike and mean midsummer (July–August) water temperature in the Bay of Quinte and eastern Lake Ontario from 1971 to 1992. The polynomial equation, correlation coefficient, and probability level are provided. Years are indicated. Mean daily water temperature was measured in the Bay of Quinte at the Belleville, Ont., water filtration plant.

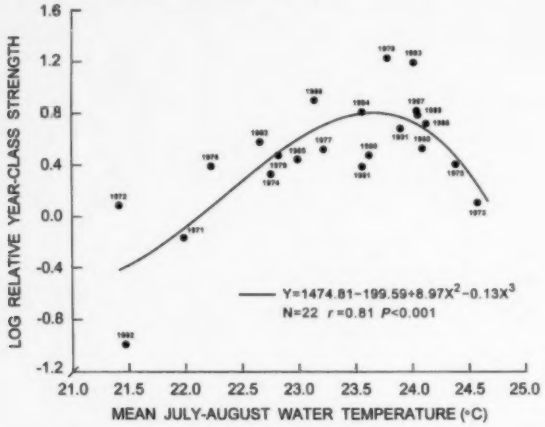
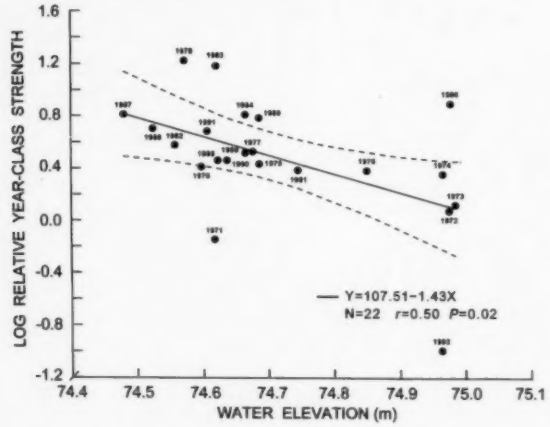


Fig. 6. Relation between the logarithm of the proportional size of the year-class of northern pike and mean late summer - early autumn (August–October) water elevation in the Bay of Quinte and eastern Lake Ontario from 1971 to 1992. Regression equation, correlation coefficient, and probability level are provided. The years are indicated, and the dashed curves delineate the 95% confidence limits. Water elevation was measured in eastern Lake Ontario at Oswego, N.Y.



and water elevation for the open-water period, March–December, were examined.

Two year-classes, 1978 and 1983, dominated during this period (Fig. 4). The 1978 year class appeared after a substantial winter mortality during two successive winters, 1976–1977 and 1977–1978, affected the fish community. There is evidence that the extreme strength of this year class

Table 3. Correlation between mean monthly change in water elevation (m) in eastern Lake Ontario and logarithm of the proportional size of the year-class of northern pike from the Bay of Quinte and eastern Lake Ontario for the open-water period (March–December) from 1971 to 1992.

	Elevation relative to open water mean (m)			
Month	Mean	95% CI	r	P
March	–0.11	0.09	0.114	ns
April	+0.10	0.09	0.105	ns
May	+0.25	0.09	–0.071	ns
June	+0.28	0.10	–0.118	ns
July	+0.21	0.09	–0.226	ns
August	+0.09	0.09	–0.423	0.050
September	–0.04	0.07	–0.534	0.011
October	–0.18	0.07	–0.453	0.034
November	–0.30	0.06	0.235	ns
Decemeber	–0.31	0.06	0.323	ns
March–December	0.00	0.06	–0.155	ns

Note: Water elevations were measured at Oswego, N.Y. Probability values are provided. ns, not significant.

was related to the substantial reduction in the white perch (*Morone americana*) population (Minns and Hurley 1986). White perch are major predators on small and young fish. If there was predation by this species on northern pike, it would no doubt have occurred on young-of-the-year in the nursery habitat.

Relationships between year-class strength and water temperature were examined, using mean monthly temperature (Table 2). Overall, year-class strength was positively correlated with mean temperature of the open-water period (P = 0.023). The proportional size of the year-class was highly significantly correlated with the warmest months of the summer, July and August, when mean water temperature exceeded 23°C. The mean temperatures for these 2 months were averaged to illustrate the significance and the trend of the relationship ($P < 0.001$) (Fig. 5). The data were best fit by a curvilinear relationship that peaks between 23 and 24°C. The two strongest year classes, 1978 and 1983, were stronger than would be expected, given midsummer water temperatures in those years (Fig. 5). Since this relationship no doubt involves the first year of life, this temperature response coincides well with the growth of young-of-the-year northern pike. Maximum growth of young-of-the-year occurs at 22–23°C, whereas maximum recruitment occurs at a temperature that is only slightly higher (23–24°C).

An unexpected positive correlation was also obtained with December water temperatures (Table 2). The correlations with midsummer temperatures appear to implicate nursery rather than spawning conditions, because spring spawning time was not involved. This correlation may be related to increased growth and associated survival of young fish. The direct effect of temperature during the first year of life appears to be rather universally important (Le Cren 1987; Fortin et al. 1982). Increased summer temperature could also affect survival by increasing vegetative growth and cover.

Year-class strength and mean annual water elevation during

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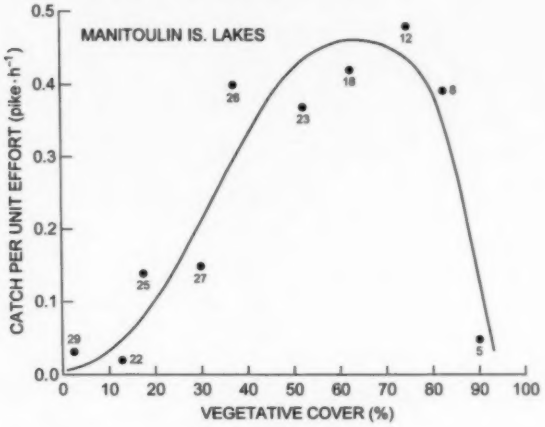
Fig. 7. Relation between catch of northern pike per unit of gill-net effort and percent vegetative cover in Manitoulin Island lakes Wickett and Smoky Hollow, in midsummer 1968–1971. Catch is expressed as the number of northern pike caught per hour in a 50-m experimental green multifilament multimesh gill net set for 24 h in various densities of vegetative cover in the two shallow (<3 m) lakes. The number of gill-net sets ($N = 195$) is indicated with each data point. Relation fitted by running averages. Vegetative cover was measured at two randomly chosen locations within 50 m of the gill net and was averaged.



the open-water period were not correlated (Table 3). Year-class strength was, however, negatively correlated with elevation for those open-water months when water levels were decreasing (August–October) from late summer to early autumn ($P = 0.02$) (Fig. 6). It is apparent that recruitment was not related to spring water elevations at spawning time. Correlations with late summer and autumn implicate effects on young northern pike in the nursery habitat. It is not readily apparent how low water elevations in late summer would influence year-class strength of northern pike, especially when the relationship was negative. These correlations are not spurious, because they are strong and show a gradually changing monthly trend (Table 3). Lower water levels in late summer and early autumn could force young fish to move offshore earlier, reducing the possibility of fall and early winter entrapment in degraded shallow backwaters (Derksen 1989). Lower water levels in late summer and early fall could increase the amount of cover present per volume of habitat, decreasing susceptibility of the fish to fall predation by other species. Decreasing water levels could also concentrate small prey species, improving growth and survival.

Juvenile and adult habitat

Adult northern pike are found in relatively shallow water in summer, usually < 4 m but sometimes as deep as 12 m, that is relatively clear, cool, and well oxygenated (> 3 $mg \cdot L^{-1}$) with some vegetative cover. Habitat and environmental requirements of juvenile (yearling to maturity) and adult northern pike are relatively well known (see review, Inskip 1982); however, their association with vegetative habitat needs to be better quantified.

To better understand the association between vegetative cover and northern pike, we analyze data from multiple experimental multimesh gill nets set in midsummer during 1968–1971 in two shallow (< 3 m) lakes, Smoky Hollow and Wickett, on Manitoulin Island. Throughout the open-water period in the two lakes, there was a range of densities of aquatic macrophytes. Plants were primarily species of *Potamogeton*, including *P. crispus*, *Ceratophyllum demersum*, and *Elodea canadensis*. The catches of juvenile and adult northern pike were low at low macrophyte densities, highest at intermediate densities (35–80%) and low in very dense, virtually continuous vegetative mats (Fig. 7). The larger pike were caught at low vegetation densities, and the smallest were taken in the densest vegetation. Randall et al. (1996) conducted littoral-zone electrofishing surveys in the lower Great Lakes and concluded from general categories that northern pike were most abundant when vegetation was moderately dense (31–70%), results that are similar to the peak abundance reported here. These independent results are similar to those of Grimm and Backx (1990, Table 5), who measured vegetative cover and biomass in six different water bodies in the Netherlands. Our quantitative results support Grimm and Backx's (1990) observation that northern pike populations require at least 30% vegetative cover.

As northern pike mature, their vegetative associations change from emergent for fry to emergent, floating, and submergent for young to submergent for adult. Northern pike are visual predators and are primarily active during the day but usually feed crepuscularly. Their "ambush" predation style requires cover, and aquatic macrophytes are preferred. Vegetation provides a refuge from predation for the young and cover to conceal feeding fish of all sizes (Inskip 1982).

Northern pike generally prefer shallow vegetated areas (Diana et al. 1977; Inskip 1982; Chapman and Mackay 1984*a*; Cook and Bergersen 1988). For a large piscivore such as northern pike, however, there is likely an advantage to exhibiting some versatility in habitat selection, depending on availability of prey and other factors. Chapman and Mackay (1984*b*) demonstrated that northern pike distribution in a moderate-sized lake in Alberta was not necessarily strongly tied to shallow vegetated areas. Although fish were associated with macrophytes more often than would be predicted if they were choosing habitats randomly, northern pike were versatile in habitat selection.

The selection and use of vegetated areas depends on the size of fish. Chapman and Mackay (1984*a*) found that large northern pike were often observed at the macrophyte - open-water interface, while small ones were rarely seen there. Grimm (1981, in Chapman and Mackay 1984*b*) found that large northern pike used open-water and vegetated areas, while smaller northern pike were restricted to more heavily vegetated areas. Chapman and Mackay (1984*a*) found that large (> 25 cm) and small (< 25 cm) northern pike differed significantly in their selection of depth but not in their selection of vegetation type. Large fish were found in deep, unvegetated waters more frequently than were small fish. Cook and Bergersen (1988) found that female northern pike occupied deeper habitats than did males of the same size.

Very dense vegetative cover appears to be suboptimal, especially for larger northern pike (Fig. 7). The boundary zone between stands of aquatic vegetation and open water may pro-

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Table 4. Examples of recent northern pike habitat restoration projects in the Great Lakes Basin.

Lake	Site	Diagnosis	Objectives	Remediation	Evaluation	References
Ontario	Bay of Quinte					
	Pine Point	Overmature *Typha* marsh	Improved spawning and nursery for northern pike	Dredged a complex of 480 m of channels 1.2–2.5 m deep, 10–15 m wide (1993)	No assessment of northern pike spawning (1993); YOY northern pike found in summer (1993)	1,2,3
	Sawguin Creek	Overmature *Typha* marsh	Improved spawning and nursery habitat	Dredged a complex of 380 m of channels, removing the entire root mass, ensuring 1-m depth; channel edge slope 1.5:1 (1992)	No assessment of northern pike spawning (1993); YOY northern pike found in summer in 1994, YOY northern pike found in dredged but not in natural channels; channel depth inadequate to maintain DO and temperature requirements	1,2,3
	Toronto Shoreline					
	Mimico Creek	Loss of wetlands	Wetland creation	Planted species of emergent vegetation using triangular log cribs, fibre pots, and individual plantings; installed fencing to exclude carp and minimize disturbance	Slow to establish due to continuing hydrological effects on sediment	4,5,6
	Bluffers Park	Loss of wetlands	Wetland creation	As above	Washed out due to wave action from lake; failed to address stormwater flow and wave action effects	4,5,6
	Toronto Islands	Loss of wetlands	Create northern pike spawning	Three cuts in barrier berm to allow fish passage; hummocks created and seeded with soft-stem vegetation (1992)	Northern pike observed in 1994; no YOY documented; YOY likely dispersed rapidly to lagoon system as temperature and DO became suboptimal	4,7,8
	Hamilton Harbour	Declines in water levels limit recruitment; lack of vegetation	Maintain water levels until fry dispersed; reestablish vegetation	Installed water control structures and excluded carp from some ponds (1994)	Where carp excluded, transparency increased and rooted vegetation established; 6-yr monitoring program planned	9
Superior	Thunder Bay					
	Neebing–McIntyre Floodway	Habitat destroyed by filling	Recreate spawning, nursery, adult habitat	Excavated four 20-m embayments into sides of floodway; planted banks with willow (1991)	More fish in channels than in floodway; not known if actual increase in production or only attraction of fish (1992, 1993)	10
	McVicar Creek	Wetland lost; failed to reestablish due to wave action	Create shelter from wave action	Created 175-m rock island (1992)	Newly established vegetation at most sample sites; no northern pike documented in 1993	10

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Table 4 *(concluded).*

Lake	Site	Diagnosis	Objectives	Remediation	Evaluation	References
	McKellar River	Wetland lost	Reestablish wetland	Created two 1-ha lagoons by excavating the riverbank; planted trees, shoreline cover and macrophytes (1994)	Extensive use by northern pike in 1995	10
Inland	Wilcox Lake	Wetland loss and physical exclusion of spawners; recruitment failure	Create new wetland in senescent marsh	Dredged a 50 × 40 m grid of channels 2–4 m wide; dredging spoils used to elevate a grid of similar mounds; seeded (1986)	Used by spawning fish; egg deposition and juvenile production estimated; after 2–3 yr natural succession, slumping channel banks and sedimentation from wave action had reduced available habitat	11, 6
	Creek between Butterfly and Minnitaki lakes	Altered nursery habitat with dredging spoils from channelizing length of waterway	Reduce nursery habitat alteration and stabilize clay spoil spit	Cut spoil spit and create spawning hummocks	Hummocks were built and aerially seeded, reducing erosion; northern pike use was not assessed	12

Note: The reasons for the restoration program, the specific objectives, the remedial action, and evaluation of the outcome are provided. The references for the table are numeric and are as follows: (1) Anonymous 1993*a*; (2) K. Hartley, Moira River Conservation Authority, R.R. 2, Belleville, Ont., personal communication; (3) L. Cope, OMNR, 1 Richmond Boulevard, Napanee, Ont., personal communication; (4) Anonymous 1993*b*; (5) Anonymous 1993*c*; (6) I. Buccanan, OMNR, 10401 Dufferin Street, Maple, Ont., personal communication; (7) Anonymous 1992; (8) R. Strus, Metropolitan Toronto Region Conservation Authority, c/o OMNR, 10401 Dufferin Street, Maple, Ont., personal communication; (9) K. Minns, Department of Fisheries and Oceans, P.O. Box 5050, Burlington, Ont., personal communication; (10) E. Iwachewski, OMNR, P.O. Box 5000, Thunder Bay, Ont., personal communication; (11) Reid 1990; (12) F. Cole, OMNR, P.O. Box 309, Sioux Lookout, Ont., personal communication.

vide important edge, affording ambush hunting sites (Reighard 1915, in Inskip 1982; Chapman and Mackay 1984*a*).

Changes to the amount of vegetation affect distribution. Cook and Bergersen (1988) found that northern pike abundance varies in response to changes in macrophyte density and distribution. In a year when macrophyte growth increased near shore, fish frequented those areas more than in the previous year. Cook and Bergersen noted that with an increase in macrophyte growth, fish remained in shallower water, closer to shore. However, Holland and Huston (1984) found that juvenile northern pike avoided very dense macrophyte beds, and they speculated that low oxygen levels associated with these vegetative mats may have caused that behaviour. In winter, northern pike tend to occupy deeper habitats as ice cover and die-back of vegetation change the inshore habitat and oxygen depletion commences (Casselman 1978; Cook and Bergersen 1988; Derksen 1989).

Macrophyte density influences the size structure of northern pike populations. Since large fish require more open water and vegetation – open-water interface, lakes with dense vegetation are usually dominated by smaller northern pike (Grimm and Backx 1990).

Northern pike exhibit a preference for type and density of vegetation. In Eleven Mile Reservoir, Colorado, Cook and Bergersen (1988) found the most abundant and widespread species to be *Ceratophyllum demersum*, *Elodea canadensis*, *Potamogeton* spp., and *Chara* spp. Males preferred areas of *Potamogeton* spp. in combination with other macrophytes, while females preferred stands of *Potamogeton* spp., *Elodea canadensis*, or *Ceratophyllum demersum*.

Temperature is an important environmental factor affecting this cool-water fish (Casselman 1978). The physiological growth optimum for yearlings to adults fed ad libitum was 19°C for biomass and 21°C for length. When fish 2 and 3 yr old from the laboratory and from studies in the natural environment were compared, the optimum temperature for linear growth for laboratory fish was 20.9 ± 0.1°C and under natural conditions, 19.8 ± 0.6°C (Casselman 1978). This slight difference was attributed to available food and feeding rate, which directly affect optimum temperature for growth.

Laboratory studies indicate that the final preferred temperature of northern pike is slightly higher (2 or 3°C) than the optimum for growth (McCauley and Casselman 1981). Headrick and Carline (1993) used temperature-sensitive radio transmitters on adult northern pike in two southern Ohio impoundments and showed that, when water temperature exceeded 20°C, fish sought a cooler average temperature but that they sought significantly cooler temperatures only when the surface exceeded 25°C. However, once the surface temperature reached 25°C, the coolest available water with > 3 $mg \cdot L^{-1}$ dissolved oxygen was 25°C. Adult fish lost weight during this period of habitat constriction.

Juvenile and adult northern pike can tolerate a broad range of temperatures. The upper incipient lethal of subadult north-

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ern pike was 29.4°C in the laboratory (Casselman 1978) and over 30°C in the natural environment (Ridenhour 1957). The lower incipient lethal temperature has not been measured. Casselman (1978) observed, however, that northern pike showed no apparent stress when subjected to temperatures as low as 0.1°C prior to freeze-up in shallow lakes.

Water transparency can affect body condition of northern pike (Craig and Babaluk 1989). The authors showed that weight of a northern pike was positively related to Secchi depth. With every increase in Secchi depth of 1 m over the 3-m range, the fish's weight increased 6%. Craig and Babaluk concluded that high turbidity during the open-water period in prairie lakes in Canada reduced the ability of northern pike to feed.

Food consumption, conversion efficiency, and growth rate are maximal when oxygen saturation is 100%; any decrease in oxygen concentration directly affects growth (Adelman and Smith 1977). Feeding decreases markedly when oxygen concentration falls to approximately 2–3 $mg \cdot L^{-1}$ (20–30% air saturation) and ceases below 2 $mg \cdot L^{-1}$.

Under the ice, the concentration of dissolved oxygen affects activity and vertical distribution of northern pike. In shallow, eutrophic water bodies, as the oxygen is progressively depleted during winter from the substrate to the ice-water interface, the fish move increasingly higher in the water column to the bottom of the ice sheet (Casselman 1978). This behaviour has been studied in the natural environment (Magnuson and Karlen 1970) and under simulated winter conditions in the laboratory (Petrosky and Magnuson 1973). When oxygen concentration decreased to approximately 2–3 $mg \cdot L^{-1}$, northern pike approach the ice-water interface. At oxygen concentrations below that level, there was a noticeable decrease in activity (Casselman 1978). In winter under the ice, northern pike stop feeding when oxygen concentration reaches approximately 2 $mg \cdot L^{-1}$. When oxygen concentrations are low (< 4 $mg \cdot L^{-1}$), some fish actively seek higher levels. From observations in the natural environment by Headrick and Carline (1993) on restricted summer habitat and by Casselman (1978) on restricted winter habitat, adult northern pike attempt to avoid oxygen concentrations of < 3–4 $mg \cdot L^{-1}$. Johnson and Moyle (1969) observed that northern pike were attracted to an aerated discharge when oxygen concentrations under the ice were < 1 $mg \cdot L^{-1}$. However, under winter conditions, northern pike were extremely inactive at oxygen concentrations below 0.7 $mg \cdot L^{-1}$ (Casselman 1978). Casselman captured live northern pike in stationary gear at oxygen concentrations as low as 0.04 $mg \cdot L^{-1}$ (0.3% air saturation).

Depending upon temperature, the upper range of the lower incipient lethal oxygen concentration is 0.5–1.5 $mg \cdot L^{-1}$ (Casselman 1978). Winterkills of northern pike in the natural environment resulting from critically low winter oxygen levels are selective (Casselman and Harvey 1975; Grimm 1983). The fish that died were usually significantly larger, older, and faster growing than the ones that survived. As well, significantly more females than males died.

It is apparent that vegetative cover, temperature, oxygen, water transparency, and light intensity interact to affect the physiology of the fish. These must be taken into consideration when examining and restoring northern pike habitat, and many of the restoration projects that have been conducted, especially those associated with spawning, have taken these specific requirements into consideration.

Habitat restoration in the Great Lakes Basin

Restoration of northern pike populations through habitat manipulation has usually focused on spawning habitat. The use of dikes or low-head dams in wetlands, marshlands, and swamps to control water level to create and manage northern pike spawning marshes is well established (Franklin and Smith 1963; Forney 1968; Kleinert 1970; Williams and Jacob 1971; Fago 1977). Such managed marshes can increase recruitment over that from unmanaged spawning areas and can compensate, at least in part, for historical losses of wetlands (Kleinert 1970).

In the Great Lakes Basin, recent habitat restoration projects for northern pike have focused on spawning and nursery habitat but generally have not been of the "managed marsh" type (Table 4). We summarize, describe, and evaluate some examples of recent restoration projects that have been conducted in the Great Lakes Basin (Table 4). These projects involve attempts to either improve or create existing or new habitat or wetlands where historical ones have been lost or altered. Habitat improvement has been attempted by cutting channels in senescent *Typha* marshes, controlling water levels, and excluding carp to allow reestablishment of vegetation (e.g., Bay of Quinte, Hamilton Harbour; Table 4). Habitat creation projects have involved planting emergent vegetation, using a variety of planting techniques, excluding carp from the new sites, reclaiming a trout pond by allowing access for northern pike, excavating upland channels, altering dredging spoils, and changing site hydrology (e.g., Toronto shoreline, Lake Superior, Wilcox Lake, Butterfly and Minnitaki lakes; Table 4).

Assessing the restoration of northern pike habitat

Successful habitat restoration efforts must include clear objectives, measurable criteria, and a well-planned assessment program. The latter was often lacking. For northern pike habitat restoration projects, the specific habitat requirements that are limiting must be identified and restoration must focus on meeting those requirements. Clearly, planning for such projects must take into account all factors contributing to the quality and quantity of northern pike habitat, including location and size of the habitat, water levels, site elevation, and morphometry, as well as accessibility. New habitats should be constructed not only with the species' requirements in mind but also with a view to facilitating future assessment (e.g., ease of observing use and enumerating spawners and juveniles; Reid 1990).

Most of the northern pike habitat projects reviewed target both spawning and nursery habitat (Table 4). The distinction between the habitat requirements for each of those life stages has not been clearly defined in the planning nor has a rigorous attempt been made to determine factors limiting production. In most cases, the objectives and criteria for success of these projects have not been strictly defined. Similarly, most assessment efforts have not strictly matched measurement require-

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ments (what to measure and at what scale) with stated objectives.

As a result, we have found it difficult to evaluate whether these projects resulted in improved habitat for northern pike and ultimately in increased production. It is surprising that habitat restoration for this species has not been more quantitatively evaluated, since habitat requirements are much better defined for this species than for most. In several instances, failure to plan for all factors influencing habitat dynamics at the site compromised the potential for success. Often this was because of factors operating at different spatial or temporal scales. For example, larger-scale hydrological effects must be addressed in advance if new patterns of sedimentation and vegetation distribution are desired. Natural changes of the site over the long term must also be considered; several projects (Table 4) suffered from deterioration of the site over time, particularly the settling of bank slopes (e.g., Bay of Quinte, Wilcox Lake), sedimentation (Mimico Creek), movement of dislocated marsh into new channels (Bay of Quinte), and excessive vegetation growth (Wilcox Lake, Bay of Quinte).

These problems point to three important restoration requirements. First, some sites may require a continuous process of rejuvenation to ensure suitability for northern pike and other species. More importantly, attempts to restore habitat at sites with dense, pure stands of cattail, for example, may need to be more aggressive than at first appears. The natural succession of such sites, coupled with the settling of newly disturbed sediments, may require that channels be initially constructed deeper and wider than "optimum" for northern pike.

Second, the case studies described here (Table 4) point to the need to consider all factors that might influence the site. Failure to consider and plan for the full range of natural and human factors, particularly the hydrology of the area, may jeopardize the success of any project. In this sense, project plans must examine the requirements at a variety of physical and temporal scales to understand the dynamics of the site before and after restoration.

Third, restoration projects require thorough assessment and documentation so that the contribution can be evaluated, preferably quantitatively. This is necessary not only to evaluate and document restoration success but also to document unforeseen outcomes so that future attempts and projects can benefit from the experience, regardless of the results. Long-term followup would be extremely useful to completely evaluate the extent and duration of the contribution. It is also apparent that precise and detailed knowledge now exists to evaluate habitat requirements of northern pike. It follows that precise, quantitative data must be collected when assessing habitat if interpretations and predictions are to be accurate.

When designing and implementing habitat restoration projects for northern pike, it is important to realize that habitat changes, either predicted or unpredicted, could affect, displace, or even eliminate other species.

Important habitat requirements and critical factors

Considering habitats used by northern pike, spawning has received the greatest amount of attention and is best understood. Physical habitat features have been reconstructed and altered in restoration programs with moderate success. Manipulation of managed northern pike marshes has reached such a level that use and production can exceed those of natural conditions (Williams and Jacobs 1971). Indeed, it is possible to convert dry ground to wetlands that northern pike will use for spawning and nursery habitat (Reid 1990). Other artificial habitats have been created successfully. Gillet (1989) created artificial floating substrates that attracted spawning northern pike. Egg deposition was high, exceeding $1000 \cdot m^{-2}$, on structures that were anchored away from shore. The creation of artificial habitat must be carefully evaluated because, although it may increase the presence of one life stage, this may not result in an overall increase in productivity and may also displace other ecologically important species not currently considered to be important or to have human-valued priority.

Year-class strength of northern pike over the past 22 yr in the Bay of Quinte has not been correlated with spring water elevations, as has frequently been observed for other populations (e.g., Johnson 1957; Masse et al. 1993). Even though the fluctuations were relatively extreme over this period, spawning and recruitment were less important in influencing year-class strength than were summer conditions associated with young northern pike and nursery habitat. Also, the strength of the 1978 and 1983 year-classes indicates that adequate spawning and reproductive potential existed in the northern pike population of the Bay of Quinte and eastern Lake Ontario even though numbers were at record low levels (J.M. Casselman, unpublished data).

These observations support our contention that, contrary to general belief, spawning habitat requirements are usually less critical or limiting than heretofore considered. Furthermore, these requirements are relatively well understood, and spawning habitat is more easily manipulated and restored. Minns et al. (1996) reached a similar conclusion through simulation modelling. They contended that fry and juvenile-adult habitat supplies are more limiting than spawning habitat. There is no doubt that since European settlement, the extensive loss of marshes and wetlands along the shores of the Great Lakes (Whillans 1979, 1982; Dodge and Kavetsky 1994), especially Lake Ontario, has reduced and, in some situations, virtually eliminated northern pike recruitment. If northern pike are to become abundant again in Great Lakes embayments, then this trend must be reversed. Although restoration of spawning habitat is important, we consider that it is not the major factor limiting rehabilitation of northern pike stocks in the Great Lakes but that reestablishment of macrophyte habitat and cover is more important.

Macrophyte cover is an important feature of nursery habitat that not only reduces susceptibility to predation but also provides cover for important prey species and for young pike to lie in wait for prey. We conclude that optimal vegetative densities for nursery habitat range from 40 to 90%. Turbidity and eutrophication can reduce transparency and affect feeding, but more importantly and critically, can also reduce light penetration, inhibiting macrophyte growth. This is important not only for young-of-the-year pike but also for juveniles and adults. Loss of cover can expose young northern pike to predation; our study of year-class strength provides circumstantial evidence that predators in the nursery habitat, such as white perch, can affect survival of young-of-the-year survival and yearling recruitment. Since year-class strength was correlated with temperature, especially in midsummer, temperature may

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directly affect growth and enhance survival of young northern pike, by increasing vegetative cover. Nevertheless, this 22-yr case history study of year-class strength demonstrates the importance of midsummer nursery habitat conditions on northern pike production.

Catch and abundance of adult northern pike was related to the extent of macrophyte cover. Larger individuals frequent lower densities; smaller individuals, higher densities. Optimal juvenile and adult habitat requires vegetative cover that ranges from 35 to 80% (Fig. 7). This agrees with Grimm's (1989) observation that a water body must contain more than 25% submerged macrophytes for a northern pike dominated fish community to exist.

Abundance of vegetation is inversely related to turbidity, eutrophication, and algal production. In recent years, macrophyte production on the south shore of Lake Ontario has increased in one location (Makarewicz and Dilcher 1988). This coincided with a significant decrease in turbidity from the late 1970s to the early 1980s. Makarewicz and Dilcher concluded that the reestablishment of macrophytes was probably associated with phosphorus-abatement programs in Lake Ontario. Decreased turbidity allowed increased light penetration and macrophyte resurgence. With increased vegetative cover, northern pike feeding would be enhanced and their condition factor would improve. Macrophyte biomass and diversity were greater in the large bays of Lake Ontario (e.g., Bay of Quinte) prior to anthropogenic loading of phosphorus (Bristow et al. 1977; Warwick 1980). There is no doubt that cultural eutrophication in the mid–1950s caused reduced light penetration, decreasing and virtually eliminating vegetative cover, greatly reducing northern pike habitat and abundance (e.g., Bay of Quinte; Hurley and Christie 1977). Jagtman et al. (1990) demonstrated that eutrophication can cause loss of littoral-zone vegetation with the disappearance of northern pike habitat. From data from the late 1980s, Loftus et al. (1992) estimated that 34.7% of the Bay of Quinte supported submerged macrophytes and that Remedial Action Plan options (Hartig 1993) would increase average coverage by only 11%. However, from the relationship between catch and vegetative cover (Fig. 7), this change in vegetative cover could increase northern pike abundance by an additional 35%. It is apparent that if northern pike abundance is to be increased in the Great Lakes Basin, water transparency and macrophyte cover must be improved.

Climate warming could increase available nearshore habitat in the Great Lakes for cool-water fish (Meisner et al. 1987) such as northern pike but would make shallow embayments less optimal as juvenile and adult habitat, although probably more optimal as nursery habitat. If increased temperature causes increased vegetative growth and if macrophytes expand, northern pike abundance will do the same. If zebra mussel (*Dreissena polymorpha*) expansion in the inshore waters and embayments in the lower Great Lakes increases water transparency and leads to more macrophyte cover, more optimal nursery and juvenile-adult habitat will be restored and northern pike production improved. However, increased light penetration could increase water temperatures, having obvious effects on growth and production. An increase in macrophytes would probably result in increased organic degradation and associated biological oxygen demand, and in severe winters, with thickened ice cover, critical oxygen depressions could occur and become locally severe in confined embayments. This could result in selective winter mortalities (Casselman and Harvey 1975) of northern pike and other species. Increased macrophyte cover would not only increase northern pike abundance but could also make it more variable.

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Is fish species richness at sites in the Canadian Great Lakes the result of local or regional factors?

John R.M. Kelso and Charles K. Minns

Abstract: We tested the hypothesis that fish species representation at Canadian Areas of Concern (AOC) is similar to that at other Great Lakes locations. Clustering of fish species presence–absence from electrofishing data for 15 AOCs, data collected by a variety of methods and stored in the Ontario Fish Species Distribution Data System for the 15 AOCs and for 12 non-AOC sites indicated that (1) Fish Species Distribution Data System species lists were longest and electrofishing species lists were shortest at AOCs; (2) species lists were longer for AOCs than non-AOCs; (3) only two site groups occurred in the Great Lakes; (4) species patterns follow a lower to upper lakes pattern that relates closely to the regional groupings previously interpreted in relation to postglacial dispersion; (5) particular species were not key elements in contributing to site groupings; and (6) clustering of sites by chemical and physical characteristics and by perturbation produced groupings that differ from site groupings by fish species assemblage. From these analyses we infer that fish species representation at a location in the Great Lakes is primarily related to regional and biogeographical factors and that remediation at AOCs may contribute little to changing local species richness.

Résumé : Nous avons voulu vérifier l'hypothèse selon laquelle les espèces de poisson sont aussi bien représentées dans les secteurs de préoccupation (SP) canadiens que dans les autres secteurs des Grands Lacs. Nous avons utilisé à cette fin des données obtenues par pêche électrique dans 15 SP, groupées selon la présence ou l'absence de chaque espèce de poisson, ainsi que des données obtenues par diverses méthodes dans 15 SP et 12 autres secteurs, stockées dans le Fish Species Distribution Data System de l'Ontario. Nous avons ainsi constaté que: (1) dans le cas des SP, les listes d'espèces du Fish Species Distribution Data System étaient les plus longues et les listes d'espèces capturées par pêche électrique étaient les plus courtes; (2) les listes d'espèces étaient plus longues pour les SP que pour les autres secteurs; (3) seulement deux groupes de stations étaient discernables pour les Grands Lacs; (4) entre les Grands Lacs d'amont et d'aval, les espèces se répartissaient selon une tendance étroitement liée aux regroupements régionaux obtenus auparavant dans une étude sur la dispersion postglaciaire; (5) les espèces individuelles ne contribuaient pas de manière essentielle au regroupement des stations; (6) les groupes de stations obtenus en fonction des caractéristiques physiques et chimiques et du degré de perturbation étaient différents de ceux obtenus en fonction des espèces de poissons présentes. Ces analyses nous permettent de conclure que la liste des espèces de poissons d'une station donnée des Grands Lacs dépend avant tout de facteurs régionaux et biogéographiques et que l'assainissement des SP contribue peut-être peu à la modification locale de la richesse en espèces.
[Traduit par la Rédaction]

Introduction

Ecologists assume that community organization is not governed by a single process (Dunson and Travis 1991) and recognize the role of biotic and abiotic factors operating at different spatial scales (as examples: Green and Vascotto 1978; Eadie and Keast 1984; Ricklefs 1987; Minns 1989). Minns (1989) suggested that four factors (regional, local, anthropogenic, and methodologic) all of which operate within the Great Lakes, affect measurements of species richness. To be effective, resource management actions should appreciate the dominant factors affecting community structure and operate at an appropriate scale.

The public and fishery resource managers alike have described objectives, goals and, often, targets for aquatic systems (for example, Remedial Action Plans (RAPs) developed under the Great Lakes Water Quality Agreement (GLWQA); Kelso et al. 1996; Hartig et al. 1996; lake management plans developed through the Great Lakes Fishery Commission (GLFC) and by the Ontario Ministry of Natural Resources (OMNR)). The objectives of the RAPs at most of the 43 Areas of Concern (AOC) identified in the GLWQA and through the International Joint Commission (IJC) specify either a rehabilitation of species that are either extirpated or reduced in abundance, or an alteration in the abundance of a group of species (e.g., predators, cold-water species, centrarchids in the fish community). Seventeen of the geographically defined AOCs are in Canadian or international waters, all exceed general or specific water quality objectives of the GLWQA and suffer impairment of conventional water uses. The setting of objectives for AOCs

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Fig. 1. A map of the Great Lakes region showing the location of 17 designated Areas of Concern and of 12 non-AOC areas included in this study.

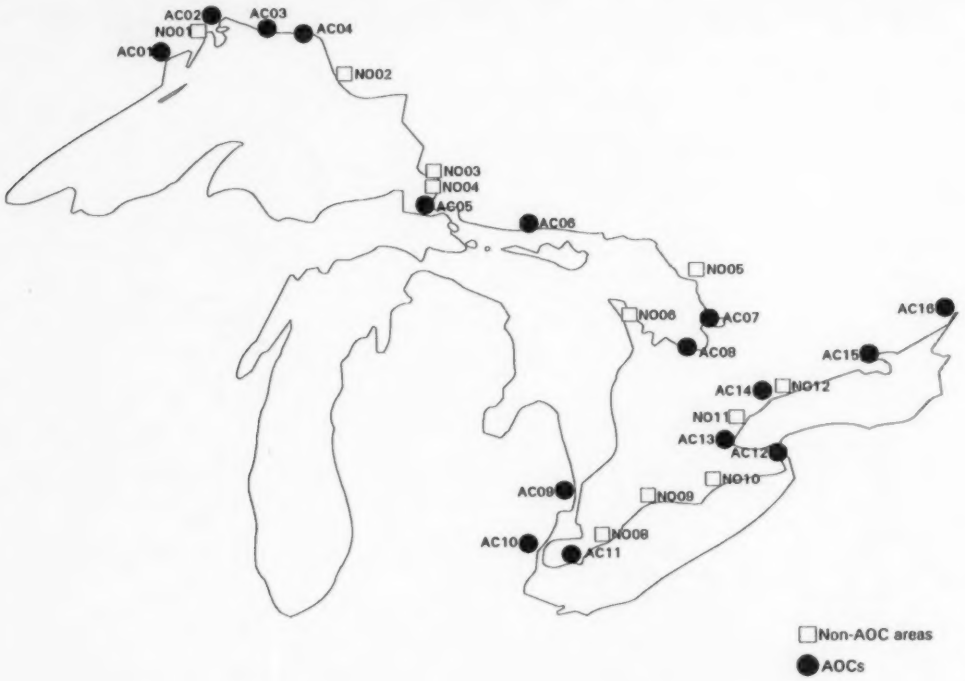

Table 1. List of beneficial use impairments used in the designation of Areas of Concern by the IJC under the GLWQA, and other sites in this study, around the Great Lakes.

No.	Beneficial use impairment
1	Restrictions on fish and wildlife consumption
2	Tainting of fish and wildlife flavour
3	Degradation of fish and wildlife populations
4	Fish tumours or other deformities
5	Bird or animal deformities or reproduction problems
6	Degradation of benthos
7	Restrictions on dredging activities
8	Eutrophication or undesirable algae
9	Restrictions on drinking water consumption
10	Beach closings
11	Degradation of aesthetics
12	Added costs to agriculture or industry
13	Degradation of phytoplankton and zooplankton populations
14	Loss of fish and wildlife habitat

assumes that localized remediation will evoke a response and lead to remediation of use impairment.

This paper addresses the hypothesis that fish community structure at AOCs is similar to the fish community structure of other locations in the Great Lakes. As a result, we test whether local, anthropogenic, or regional factors affect fish community composition and assume that methodological differences do not affect our analysis. We collected no new data and used data available from Stage 1 Reports (see GLWQA), and from the Fish Species Distribution Data System maintained by the OMNR for AOCs and from areas in the Great Lakes not targeted for remediation by the GLWQA.

Materials and methods

Study sites

There are 43 AOCs in the Great Lakes and 17 of these are in Canadian waters or in international, interconnecting waterways (Fig. 1). AOCs fail to meet the general or specific objectives of the GLWQA and have, or are likely to have, impairment of any of 14 beneficial uses (Table 1) specified in the 1987 amendments of the GLWQA. All AOCs are in embayments, estuaries, or connecting channels and are near population centres. At each AOC, citizens and government agencies have formed partnerships to develop RAPs for solving environmental problems. The RAP process for restoring beneficial uses at AOCs begins with agreement on problem definition and continues until there is confirmation that uses have been restored. Each AOC operates independently. Decentralized authority exists and is encouraged but coordination and review occur (Hartig and Law 1993) in the remediation process. However, fragmentation may impair progress toward elimination of restrictions on fish and wildlife consumption; elimination of bird or animal deformities or reproduction problems; reduction of entrophication or undesireable algae; and restoration of phytoplankton, zooplankton, fish, and wildlife populations, all of which may require some level of lakewide and regional coordination.

Data are not uniformly available at AOCs and interpretations of data and assessment of impaired uses may vary. However, data are available for the problem definition and description of causes are in draft or reviewed form. We contacted each Canadian RAP team. Of

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these 17 AOCs, Port Hope is a man-made turning basin containing contaminated sediments from radium and uranium refining operations between 1933 and 1948 and lacks a fisheries data base. The Spanish River was also excluded because of lack of relevant biological data.

Recognizing that RAPs incorporate an ecosystem approach, Hartig and Law (1993) indicated that political and geographic boundaries will have to be crossed, and impairments, causes, and restoration measures viewed within watersheds or other system boundaries. To determine if the fish community and impairments differed outside AOC boundaries we selected 12 sites (Fig. 1) not designated as areas of concern (non-AOCs). The non-AOC sites were in embayments (seven sites), at estuaries (five sites), and near population centres (seven sites). Data were not uniformly available for non-AOC sites, but we suspect this would be the case regardless of site selection. We presume that non-AOC sites were less perturbed than AOCs.

Fish species information

To test whether differences in the presence or absence of fish species existed among locations in the Great Lakes, we used three data sets: electrofishing surveys (Hamilton 1987; Dalziel 1988), the Fish Species Distribution Data System for AOCs, and data from the Fish Species Distribution Data System for 12 non-AOC sites.

Electrofishing data were available for all but three of the 17 AOCs (Spanish River, Port Hope, and Bay of Quinte) in 1986 and 1987 (Hamilton 1987; Dalziel 1988). A comparable electrofishing study was conducted in the Bay of Quinte (Minns 1990). This data set for 15 AOCs was derived from an intensive sampling effort within AOC boundaries. Information on abundance, catch per unit of effort (CUE), size ranges, and an attempt at habitat evaluation was available. At each site, sampling occurred over 2 or 3 days and the majority of AOCs were sampled once. We pooled data for all electrofishing runs at each AOC. Although the use of one sampling method enhances comparability among sites, electrofishing results are biased by differential attraction among species to the electrical current (affecting abundance estimates), ineffective sampling at depths greater than 5 m, and differential retrieval by sampler personnel.

We also used data for AOCs available from the Fish Species Distribution Data System, a centralized computer data base containing all recorded catches from the Canadian Museum of Nature, the Royal Ontario Museum, the OMNR Lake Survey Program, the OMNR Stream Survey Program, the OMNR Stream Assessment Population Analysis Program, and the OMNR AOC RAP Program (G. Gale, Ontario Ministry of Natural Resources, personal communication). Because the electrofishing studies reported by Hamilton (1987) and Dalziel (1988) were conducted by the OMNR, these data were also included in the Fish Species Distribution Data System; we eliminated those records. For this analysis, data for AOCs were extracted by citing the tertiary unit watershed code from Cox (1978). All available data were retrieved for each set of watershed codes. Although the most specific level of watershed code was used to generate the data set, data from outside the boundaries of the AOC also were retrieved. Using the Stage 1 RAP reports and the areas sampled in the electrofishing studies as a guideline, we set boundaries for data for each AOC. Generally, the confines of an AOC were limited to the nearshore lake waters and river sites no more than a few kilometres upstream from the mouth (less if any physical barriers such as dams, waterfalls, etc. existed). Using the map coordinates provided with the OMNR data, the sites were mapped and those records falling within the established boundaries of the AOCs were used to compile the species list from the Fish Species Distribution Data System for each AOC.

We identified watershed codes from Cox (1978) for the 12 non-AOC sites and data were retrieved from the Fish Species Distribution Data System as described above.

The data from the Fish Species Distribution Data System included information collected from the 1920s to 1990; however, most data were collected between 1968 and 1985 (Mandrak and Crossman 1992*a*). Sampling occurred within the entire year and a variety of collection methods were used. Collectors used an unknown combination of gill nets, seine nets, trap nets, dip nets, piscicides, angling, and electrofishing (Dodge et al. 1985). No indications of abundance, size, gear, or site characteristics are available.

State-of-the-ecosystem information

The 14 beneficial uses are outlined in the GLWQA and are summarized in Table 1. Impairments for each AOC were extracted from Stage 1 reports. We used the Ontario Guide for the Consumption of Sportfish to determine if restrictions on fish consumption were in effect at non-AOC sites, sought data from the Ontario Ministry of Environment and Energy (OMEE) that might lead to an assessment of water quality impairment, and used combined judgement of Department of Fisheries and Oceans (DFO) and OMNR staff to assess impairment in the remaining 13 beneficial uses. Table 2 lists impaired beneficial uses and provides a Great Lake assignment code for the 15 AOC and 12 non-AOC sites. Connecting channels were assumed to reflect the upstream lake except in the case of the Detroit River where we assumed a closer linkage to Lake Erie (Table 2). In addition, binary tables were assembled for the AOC sites describing (1) evidence of major contaminants present in water, soils, sediments, etc.; (2) sources of contaminants; and (3) contaminants in fish. Stage 1 reports provided the impairment listings for AOCs and data on water quality, sediment contamination, contaminant levels in fish, and potential contaminant sources. Data were reduced to binary form by indicating only whether an established objective was exceeded or not (e.g., Provincial Water Quality Objectives, OMEE Guidelines for the Open Water Disposal of Dredged Material, Provincial Fish Consumption Advisory). A negative response indicated either compliance with an objective or a lack of information. All the data were subjected to information cluster analysis.

Data analysis

Cluster analysis was used to group AOC and non-AOC sites by their fish assemblages and ecosystem state attributes such as impaired beneficial uses, contaminant exceedances, contaminant sources, and contaminants in fish. The cluster method was based on an information theory metric (Orloci 1972) described in detail by Minns (1989). The clustering criteria is a quantity which approximates χ^2. The statistic at each step is the same as Cochran's Q-test (Cochran 1950) except that new groups are formed by joining prior groups using a minimum χ^2 at each step. The χ^2 values in the cluster dendrogram are additive. The advantage of this clustering procedure is the ability to establish significance levels for clustered groups. Each binary matrix was clustered by rows and by columns. A reordering of the data matrix aided the interpretation of the groups.

Results

Fish species presence–absence patterns

Separate data sets

Clustering of AOC and non-AOC sites apparently was based on location within the Great Lakes (Tables 3, 4, and 5). Connecting waterways either clustered separately or were included with the upstream Great Lake. The electrofishing data for AOCs produced two significant ($P < 0.001$) groups (Table 3) of sites: (1) Lake Superior sites and (2) all other sites. The same data identified four significant ($P \leq 0.005$) groups of fish species. Site group 1 tends to have many of species group 2 present and species group 1.2 absent while site group 2 follows the opposite pattern (Table 3). Species group 2 includes whitefish, burbot, suckers, sticklebacks, and sculpins and species group 1.2 includes an array of species such as centrarchids, percids, cyprinids and bullheads. The clustering

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Table 2. Tabulation of beneficial use impairments for Areas of Concern (AOC) and other, non-AOC sites around the Great Lakes.

Code	Place	Great Lake	Impairment of beneficial use														No.
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Areas of Concern																	
AC01	Thunder Bay	Superior	✓	—	✓	—	—	✓	✓	—	—	✓	✓	—	—	✓	7
AC02	Nipigon Bay	Superior	✓	✓	✓	—	—	✓	✓	✓	✓	—	✓	—	—	✓	9
AC03	Jackfish Bay	Superior	✓	—	✓	—	—	✓	✓	—	✓	✓	✓	—	—	✓	8
AC04	Peninsula Harbour	Superior	✓	—	✓	—	—	✓	✓	—	—	—	—	—	—	✓	5
AC05	St. Marys River	Superior	✓	—	✓	✓	—	✓	✓	✓	—	✓	✓	—	—	✓	9
AC07	Severn Sound	Huron	✓	—	✓	—	—	—	✓	✓	—	—	—	—	—	—	4
AC08	Collingwood	Huron	✓	—	—	—	—	—	✓	✓	—	—	—	—	—	—	3
AC09	St. Clair River	Huron	✓	✓	—	—	—	✓	✓	—	✓	✓	✓	✓	—	✓	9
AC10	Detroit River	Erie	✓	—	—	✓	—	✓	✓	—	✓	✓	✓	—	—	✓	8
AC11	Wheatley Harbour	Erie	—	—	—	—	—	—	✓	—	—	—	—	—	—	—	1
AC12	Niagara River	Erie	✓	—	✓	✓	—	✓	✓	—	—	—	—	—	✓	—	6
AC13	Hamilton Harbour	Ontario	✓	—	✓	✓	✓	✓	✓	✓	—	✓	✓	✓	✓	✓	12
AC14	Toronto Harbour	Ontario	✓	—	✓	—	—	✓	✓	✓	—	✓	✓	—	—	✓	8
AC15	Bay of Quinte	Ontario	✓	—	✓	—	—	✓	✓	✓	✓	✓	✓	—	—	✓	9
AC16	Cornwall	Ontario	✓	✓	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	—	✓	12
Non-AOCs																	
NO01	Black Bay	Superior	—	—	✓	—	—	—	—	—	—	—	—	—	—	—	1
NO02	Ashburton Bay	Superior	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0
NO03	Batchawana Bay	Superior	✓	—	✓	—	—	—	—	—	—	—	—	—	—	—	2
NO04	Goulais Bay	Superior	✓	—	✓	—	—	—	—	—	—	—	—	—	—	—	2
NO05	Parry Sound	Huron	—	—	—	—	—	—	—	—	—	—	✓	—	—	✓	2
NO06	Owen Sound	Huron	✓	—	—	—	—	—	—	—	—	—	✓	—	—	—	2
NO07	Thornbury	Huron	✓	—	—	—	—	—	—	—	—	—	—	—	—	—	1
NO08	Port Stanley	Erie	✓	—	—	—	—	✓	—	—	—	—	✓	—	—	✓	4
NO09	Port Dover	Erie	✓	—	—	—	—	✓	—	—	—	—	✓	—	—	✓	4
NO10	Port Burwell	Erie	✓	—	—	—	—	✓	—	—	—	—	✓	—	—	✓	4
NO11	Oakville	Ontario	✓	—	—	—	—	✓	—	—	—	✓	✓	—	—	✓	5
NO12	Oshawa	Ontario	✓	—	—	—	—	✓	—	—	—	✓	✓	—	—	✓	5

of AOCs using the Fish Species Distribution Data System also produced two significant site groups (Table 4). Group 1 included all the Lake Superior sites except the St. Marys River. The species clustering produced eight significant ($P \leq 0.004$) groups but only species group 2.1.2.1 appeared to explain the site groupings; these species were largely absent from the Lake Superior sites and were common in the lower Great Lakes, e.g., longnose gar, gizzard shad, brown bullhead, and a variety of cyprinids. Eight of the species in group 2.1.2.1 were the same as those in group 1.2 obtained with the clustering of the electrofishing data (Table 3). The clustering of the non-AOC data set produced two significant ($P < 0.001$) site clusters and six significant ($P \leq 0.01$) species clusters (Table 5). Site group 1 contained all the upper Great Lake (Superior and Huron) sites and group 2 the lower lake sites. Absence of species from cluster groups 1.1.2 and 1.2.1 in site group 1 explained their separation from site group 2. Across the three cluster analyses of the three data sets, the most consistent cluster appeared to be that formed by the sites in Lake Superior, with an obvious but somewhat weaker grouping of sites in the remaining three Great Lakes.

Some of the differences in the three data sets may be attributable to unevenness in the completeness of sampling species of the different taxonomic groups. A species richness summary by site (electrofishing and the Fish Species Distribution Data System list for AOCs were combined) and by data source in each great lake shows taxonomic group and data source differences (Table 6). AOCs generally have longer species lists than non-AOCs: 19–78 and 15–43 species, respectively. By lake, the Fish Species Distribution Data System species list for AOCs were the longest and electrofishing lists for AOCs the shortest except in Lake Ontario where non-AOC sites had the shortest species list. By taxonomic group, salmonids were well represented at AOCs, but sparse at non-AOC sites; cyprinids, percids, and centrarchids were generally well represented at all sites (Table 6). As a result of these observations, a further set of cluster analyses was undertaken.

Cross-tabulation of species lists obtained from each data source by lake showed that the electrofishing lists for AOCs and the Fish Species Distribution Data System lists for non-AOCs were subsets of the AOC – Fish Species Distribution Data System lists (Table 7). Frequencies of species unique to one data source were compared using the McNemar test. The results showed that new species occurred significantly ($P \leq 0.004$) less frequently in AOC – electrofishing lists than in AOC - Fish Species Distribution Data System lists in all four Great Lakes (Table 7); a Bonferroni adjustment to allow for multiple testing meant that the nominal significance level, $P = 0.05$, was reduced to $P = 0.0042$. In the AOC – electrofishing data set versus non-AOC comparison, species were

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Table 3. Significant ($P \leq 0.01$) site and species clusters in the binary matrix of the AOC–electrofishing presence–absence data.

Analysis	χ^2	P	Cluster No.[a]	No. of members[b]	Description or listing of cluster membership
15 sites	139.75	<0.001	1	5	Lake Superior sites
			2	10	All other sites
50 species	94.64	<0.001	1	41	—
			2	9	Lake and round whitefish, longnose sucker, burbot, brook and ninespine sticklebacks, and mottled and slimy sculpins
	54.05	<0.001	1.1	29	—
			1.2	12	Gizzard shad, goldfish, golden shiner, brown bullhead, white perch and white bass, centrarchids (pumpkinseed, bluegill, largemouth bass, and black crappie), and freshwater drum
	31.39	0.005	1.1.1	14	—
			1.1.2	15	—

Note: Cluster numbers indicate the progressive division of the data matrix into clusters. When useful in the interpretation of the results, the membership of a cluster is listed or described.

[a]Clusters are numbered hierarchically, e.g., clusters 1.1 and 1.2 make up cluster 1, and clusters 1.1.1 and 1.1.2 make up cluster 1.1.

[b]The number of sites or species belonging to a cluster.

Table 4. Significant ($P < 0.01$) site and species clusters in the binary matrix of the AOC–Ministry presence–absence data.

Analysis	χ^2	P	Cluster No.	No. of members	Description or listing of cluster membership
15 sites	167.15	<0.001	1	4	Lake Superior except St. Mary's River
			2	11	All other sites
111 species	127.39	<0.001	1	30	—
			2	81	—
	63.93	<0.001	2.1	44	—
			2.2	37	—
	42.80	<0.001	2.2.1	16	—
			2.2.2	21	—
	41.34	<0.001	2.1.1	14	—
			2.1.2	30	—
	35.27	0.001	1.1	19	—
			1.2	11	—
	32.26	0.004	2.1.2.1	20	Longnose gar; alewife; gizzard shad; central mudminnow; golden, common, blacknose, spotfin, sand, mimic shiners; bluntnose minnow; brown bullhead; tadpole madtom; banded killifish; white bass; pumpkinseed; bluegill; smallmouth and largemouth bass; black crappie
			2.1.2.2	10	—

Note: See Table 3 for description of table format.

Table 5. Significant ($P \leq 0.01$) site and species clusters in the binary matrix of the non-AOC–Ministry presence–absence data.

Analysis	χ^2	P	Cluster No.	No. of members	Description or listing of cluster membership
12 sites	121.42	<0.001	1	7	Lakes Superior and Huron
			2	5	Lakes Erie and Ontario
70 species	69.31	<0.001	1	52	—
			2	18	—
	49.59	<0.001	1.1	28	—
			1.2	24	—
	40.64	<0.001	1.2.1	12	Brook lamprey; pink, coho, and chinook salmon; rainbow and brook trout; central mudminnow; longnose sucker; redside dace; lake chub; longnose dace; mottled sculpin
			1.2.2	12	—
	32.02	0.001	1.1.1	21	—
			1.1.2	7	Brown trout; splake; northern hog sucker; finescale dace; blackchin shiner; banded killifish; Iowa darter
	24.80	0.010	1.1.1.1	15	—
			1.1.1.2	6[1]	—

Note: See Table 3 for description of table format.

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Table 6. Summary of fish species richness data by taxonomic groupings for AOC and non-AOC sites and for Great Lakes.

	Species richness by taxonomic group						
Category[a]	Salmoninae	Coregoninae	Cyprinidae	Ictaluridae	Centrarchidae	Percidae	All spp.
AOCs							
AC01	2	3	11	0	2	4	40
AC02	5	3	6	0	0	6	33
AC03	3	2	5	0	0	3	24
AC04	5	2	3	0	0	2	20
AC05	4	2	12	1	5	5	46
AC07	3	1	12	2	5	6	43
AC08	3	0	18	1	3	4	42
AC09	3	0	18	4	9	6	58
AC10	0	0	11	2	7	5	39
AC11	0	0	3	2	5	1	19
AC12	2	1	17	6	6	9	65
AC13	4	1	16	2	7	3	48
AC14	5	2	20	3	6	7	66
AC15	3	5	21	3	6	10	78
AC16	1	0	9	2	7	5	35
Non-AOCs							
NO01	3	1	5	0	1	3	24
NO02	3	0	4	0	0	2	15
NO03	5	0	9	1	0	1	23
NO04	1	0	5	0	2	3	20
NO05	1	1	6	1	5	5	29
NO06	5	0	13	0	5	3	36
NO07	3	0	8	0	2	3	20
NO08	0	1	10	2	6	3	31
NO09	1	1	16	2	4	6	43
NO10	0	1	12	2	6	3	31
NO11	0	1	9	1	3	1	19
NO12	0	0	7	0	2	1	15
Lake by source							
Superior/ELE	4	2	10	0	4	4	38
Superior/MNR	5	3	15	1	4	6	55
Superior/NON	5	1	12	1	3	4	41
Huron/ELE	3	0	8	1	6	4	37
Huron/MNR	5	1	25	5	9	8	72
Huron/NON	5	1	16	1	6	5	49
Erie/ELE	1	0	6	1	6	3	32
Erie/MNR	1	1	18	7	8	9	68
Erie/NON	1	2	17	3	6	6	52
Ontario/ELE	4	1	9	1	6	4	42
Ontario/MNR	5	5	26	5	7	10	92
Ontario/NON	0	1	12	1	3	1	25
Great Lakes total	8	5	31	7	9	12	111

Note: Electrofishing and Ministry lists for AOCs were combined.

[a] ELE, AOC– electrofishing list; MNR, AOC–Ministry list; NON, non-AOC–Ministry list.

less frequent in AOC–electrofishing data but only significantly ($P = 0.001$) in Lake Huron. In the AOC – Fish Species Distribution Data System data versus non-AOC data comparison, new species were less frequent in non-AOC data but only significantly ($P \leq 0.001$) in Lakes Huron and Ontario. As a result, separate analyses of the AOC-electrofishing and AOC – Fish Species Distribution Data System species lists by sites were discontinued in favour of a combined species list for AOCs.

Combined data set

Using a combined (electrofishing and Fish Species Distribution Data System) species list for AOCs and the Fish Species Distribution Data System species list for the non-AOC sites, cluster analyses were then performed in three ways: (1) using all species, (2) cyprinids only, and (3) centrarchids and percids. The latter two subsets of data were selected to key upon smaller, less often observed species (cyprinids only) and larger, well known and expected species (centrarchids and

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Table 7. Cross-tabulation of species occurrences by data source for each lake and McNemar χ^2 values and probabilities for frequencies of species that occur in one data source and not the other.

(A) Cross-tabulations

Data source[a]			Lake			
AOC–Electrofishing	AOC–Ministry	Non-AOC	Superior	Huron	Erie	Ontario
Abs	Abs	—	49	35	39	18
Pre	Abs	—	7	7	4	1
Abs	Pre	—	24	39	40	51
Pre	Pre	—	31	33	28	41
Abs	—	Abs	56	54	52	55
Pre	—	Abs	14	8	7	31
Abs	—	Pre	17	20	27	14
Pre	—	Pre	24	29	25	11
—	Abs	Abs	50	32	30	18
—	Pre	Abs	20	30	29	68
—	Abs	Pre	6	7	13	1
—	Pre	Pre	35	42	39	24

(B) McNemar χ^2 values and probabilities

Data source	Superior	Huron	Erie	Ontario
AOC–electrofishing vs. AOC–Ministry				
χ^2	8.26	26.88	27.84	46.17
P	0.004	<0.001	<0.001	<0.001
AOC–electrofishing vs. non-AOC				
χ^2	0.13	4.32	10.62	5.69
P	0.719	0.038	0.001	0.017
AOC–Ministry vs. non-AOC				
χ^2	6.50	13.08	5.36	63.13
P	0.011	<0.001	0.021	<0.001

Note: A Bonferroni adjustment for multiple-testing means that $P \leq 0.004$ is equivalent to a nominal significance level of $P = 0.05$.

[a] Abs or pre, absence or presence of a number of species out of the total number (111) in a pair of data sources.

percids). The taxonomic pairing of centrarchids and percids was done to increase the number of species used to cluster sites; low numbers of species at a site or few sites with a species greatly decreases the likelihood that significant, and hence interpretable, clusters will emerge.

Pooling all fish species data produced a binary matrix of 27 sites by 111 species (Table 8). The clustering produced three ($P < 0.001$ and $P < 0.01$) groups of sites and six ($P \leq 0.001$) groups of species. The site dendrogram shows that site group 2 consists of AOC sites in Lake Superior, except for Thunder Bay and St. Marys River, plus two non-AOC sites in Lake Huron, Owen Sound and Thornbury; site group 1.1 includes all the lower Great Lakes non-AOCs plus Thunder Bay and the St. Marys River in Lake Superior, Severn Sound and Collingwood in Lake Huron, and Hamilton Harbour and Bay of Quinte in Lake Ontario; and site group 1.2 includes the Lake Erie AOCs plus Niagara River, Cornwall AOC, and the non-AOC site at Parry Sound (Fig. 2). Site group 2 is largely defined by the virtual absence of species group 2 and site group 1.2 is largely defined by absence of species group 1.2.1 and by the presence of species in group 2.2 (Fig. 3). The species groups involved are too large to warrant singling out species. However, the species patterns broadly follow the lower versus upper lakes pattern seen in the initial analyses.

The cluster analyses of taxonomic subsets led to more readily interpretable results. Using centrarchid and percid presence–absences, clustering produced two significant ($P = 0.001$) and three almost significant site groups ($P = 0.086$) and two significant ($P = 0.008$) species groups (Table 8). Species group 2 was predominantly centrarchids (7 of 13 species) while species group 1 mainly consisted of percids (6 of 8 species) (Fig. 4A). Site group 1 consisted of all Lake Superior sites plus Severn Sound (Fig. 4B). The other site groups were mixtures of sites among the lower lakes and Lake Huron AOC and non-AOC sites. Site group 1 was largely explained by absences of group 2 species. Site group 2.1 was largely separable from site group 2.2 on the basis of the presence of bluegill and the absence of darters.

The clustering of cyprinids produced another set of site groups (Table 8). Site group 2 consists of all the connecting channel AOCs plus Severn Sound and Hamilton Harbour while site group 1 subgroups are mixed geographically and between AOC and non-AOC (Fig. 5B) designations. The species groupings were not readily interpretable; however, site group 2 was largely caused by absences of species group 1.2, which includes hornyhead chub, golden shiner, common shiner, spotfin shiner, sand shiner, mimic shiner, bluntnose minnow, fathead minnow, and striped shiner. Site group 1.1 was largely explained by the presence of finescale dace, brassy minnow, blackchin shiner, and pearl dace from species group 2 (Fig. 5A).

It may not be individual species that contributed to forming

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Table 8. Significant ($P < 0.01$) site and species clusters in the binary matrices of the presence–absence data from all sources at AOCs and non-AOCs for all fish species, centrarchids and percids only, and cyprinids only.

Data set and analysis	χ^2	P	Cluster No.	No. of members	
All species at all sites					
27 sites	214.49	<0.001	1	18	See Figure 3
			2	9	
	146.86	0.011	1.1	11	
			1.2	7	
111 species	173.45	<0.001	1	47	See Figure 2
			2	64	
	108.37	<0.001	2.1	31	
			2.2	33	
	72.73	<0.001	1.1	17	
			1.2	30	
	55.61	0.001	2.1.1	14	
			2.1.2	17	
	55.36	0.001	1.2.1	15	
			1.2.2	15	
Centrarchids + percids at all sites					
27 sites	45.21	0.001	1	11	See Figure 4B
			2	16	
	29.10	0.086	2.1	9	
			2.2	7	
21 species	46.53	0.008	1	13	See Figure 4A
			2	8	
Cyprinids at all sites					
27 sites	63.75	<0.001	1	20	See Figure 5B
			2	7	
	44.49	0.043	1.1	9	
			1.2	11	
31 species	58.27	<0.001	1	16	See Figure 5A
			2	15	
	41.94	0.025	1.1	7	
			1.2	9	

groups of sites developed by the cluster analysis but rather the presence or absence of groups of species. Salmonines and coregonines are often the most economically important species and may be more susceptible to perturbations; therefore, their abundance strongly impacts fisheries management policies. We, therefore, clustered the AOCs on the basis of the presence or absence of the coregonine and salmonine species in the Great Lakes. Cluster analysis indicated an essentially random grouping of the AOCs indicating that salmonids and coregonids were not responsible for the associations among sites that resulted from cluster analysis of the entire data set.

Mandrak and Crossman (1992*b*) presented a series of regional groupings for 117 native freshwater fish species found in Ontario, interpreted in relation to postglacial dispersal. A cross-tabulation of their regional groupings with the six species clusters obtained with the combined data set for the Great Lakes shows there is strong regional element in the membership of the clusters (Table 9). Regional affinities were not reported for 8 of the 111 species and the 9 nonindigenous species used in our study, leaving 94 species assigned to one of the six groups identified by Mandrak and Crossman. The species in cluster group 1 account for the majority (27 of 33) of the ubiquitous species with group 1.2.1 having the most (11). Cluster group 2 accounted for 17 of 21 of the species confined to the Great Lakes and Nelson River drainages with cluster group 2.1.2 accounting for 9 alone. Cluster group 2.1 contains 9 of 16 species with southern Ontario distributions. Cluster group 2.2 contains 11 of 14 southwestern Ontario species and most of the eastern Ontario and miscellaneous (species with patchy widespread distributions) groups.

To determine if any apparent trend through time existed within an AOC the Fish Species Distribution Data Systems data set was sorted by decade (Fig. 6). The time span of the available data ranged from 1900 to 1980. There appeared to be random losses and gains in species with no apparent trend through time. Occasionally groupings of decades existed, usu-

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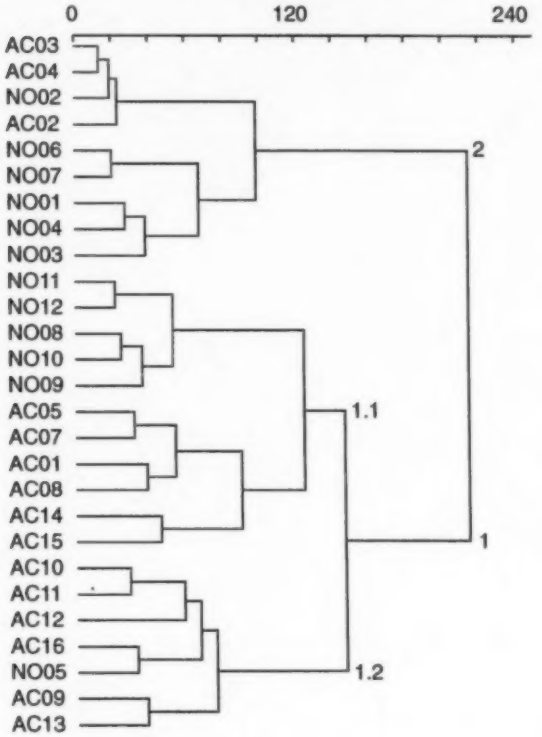
Fig. 2. Cluster dendrogram of AOC and non-AOC sites based on the combined species lists ($N = 111$). The cluster numbers correspond to those given in Table 8. (In all the dendrogram figures, the scale of the dendrogram corresponds to the χ^2 measure of the dissimilarities between clusters.)



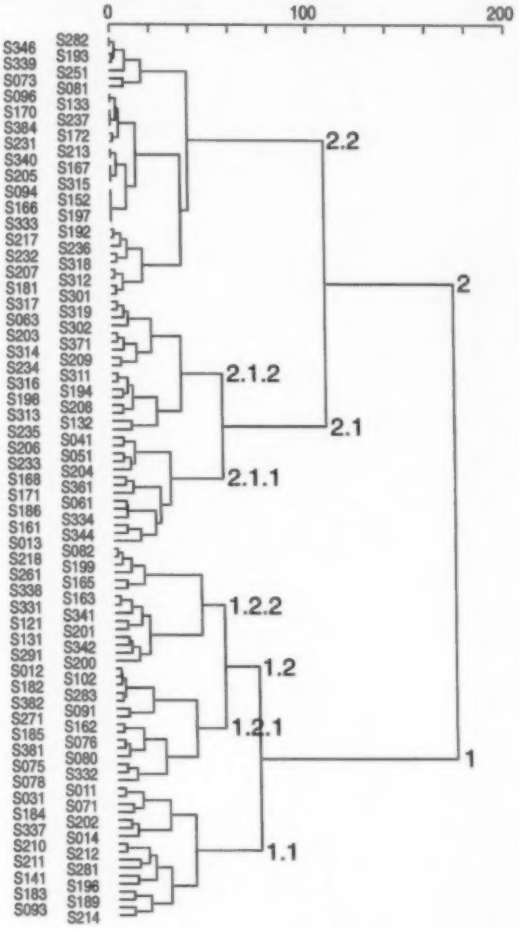
ally within data-poor AOCs, e.g., Nipigon Bay, Detroit River. On clustering data, the site groupings by decade appeared to be related to the number of species found in that decade. In other words, those decades with less available data, and therefore fewer species, tended to cluster together.

We examined species lists for each lake to determine if particular fish species were a common uniting element in each group. The key species common to Lake Superior AOCs were the longnose sucker and ninespine stickleback. Both species were found consistently in the Lake Superior AOCs and rarely elsewhere. The longnose sucker occurs throughout the Great Lakes (Scott and Crossman 1973); however, its abundance varies. The ninespine stickleback is a more northerly species but occurs in all of the Great Lakes with the exception of Lake Erie. The green sunfish was present only in Wheatley, Detroit, and St. Clair in the electrofishing and Fish Species Distribution Data System sets. The Canadian occurrence of this species is restricted to a disjunct Ontario distribution including several lakes in Quetico Provincial Park (Hudson Bay drainage basin) and areas of southwestern Ontario (Mandrak and Crossman 1992*a*). No other key species were readily apparent for the remaining lakes.

Ecosystem perturbations

Differences in fish species composition might be related to differences in anthropogenic stress. To explore this possibility, the parameters established for each AOC and non-AOC site were subjected to cluster analysis to look for evidence of site groupings.

Fig. 3. Cluster dendrogram of all species presence–absence at all AOC and non-AOC sites ($N = 27$). The cluster numbers correspond to those given in Table 8.



Reported (for AOCs) and assigned (for non-AOCs) beneficial use impairment patterns differ between AOCs and non-AOCs (Table 2). Except for Wheatley Harbour, AOCs have 3–12 use impairments with 10 sites having 7 or more, while non-AOC sites have 0–5 with the lower Great Lakes' sites having a higher number of impairments. At AOCs, the most prevalent impairments are restrictions on dredging activities and on fish and wildlife consumption. At non-AOCs, the most prevalent impairments are for fish and wildlife consumption followed by degradation of aesthetics and loss of fish and wildlife habitat.

Cluster analysis of use impairments at all sites produced two site groups significant at $P = 0.001$ (Table 10). Group 1 consisted of all AOCs plus the four non-AOCs in Lake Superior. The dendrogram shows how the site clusters were assem-

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Fig. 4. Cluster dendrograms of (A) species and (B) sites based on the presence–absence of centrarchid and percid species ($N = 21$) at all AOC and non-AOC sites ($N = 27$). The cluster numbers correspond to those given in Table 8.

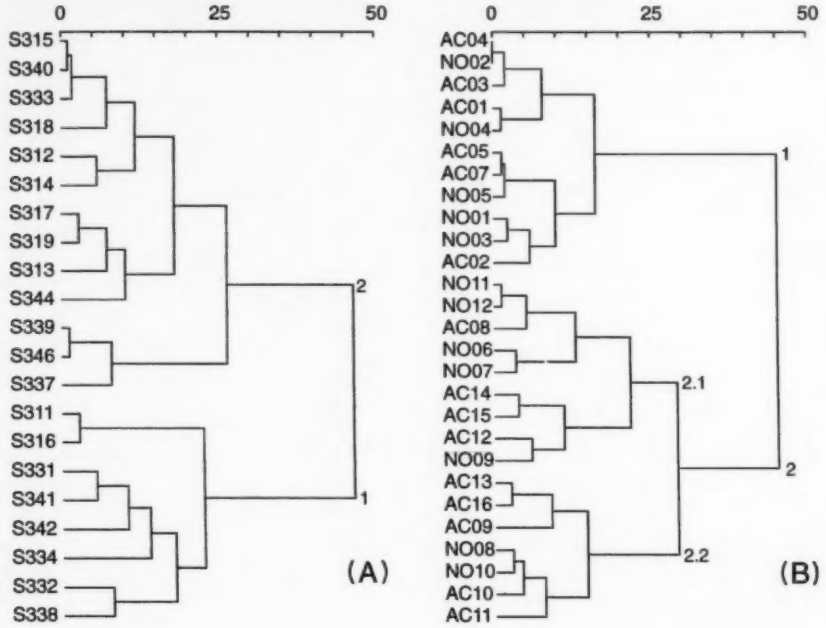

Fig. 5. Cluster dendrograms of (A) species and (B) sites based on the presence–absence of cyprinid species ($N = 31$) at all AOC and non-AOC sites ($N = 27$). The cluster numbers correspond to those given in Table 8.

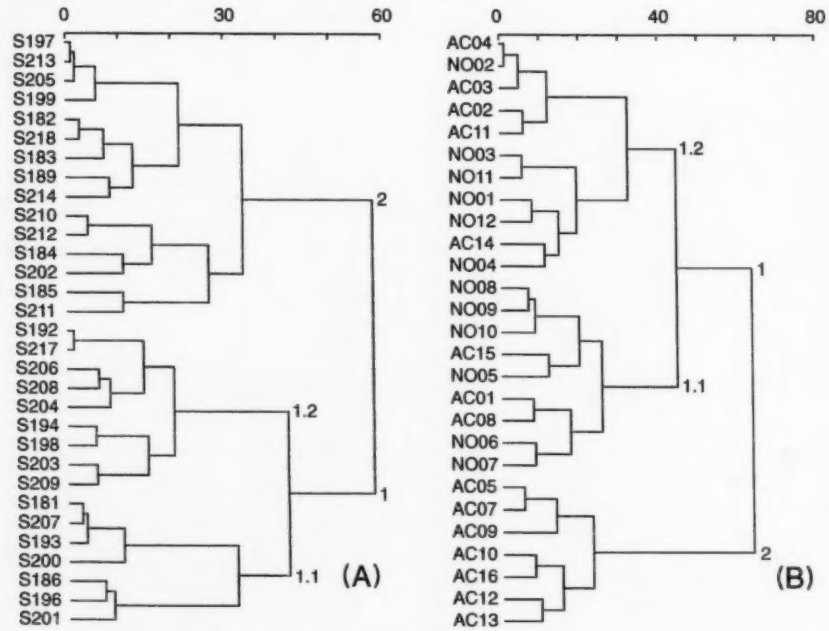

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Fig. 6. The change in number of species by decade in the Fish Species Distribution Data for AOCs. The number of species found in 1980 was used as the reference decade.

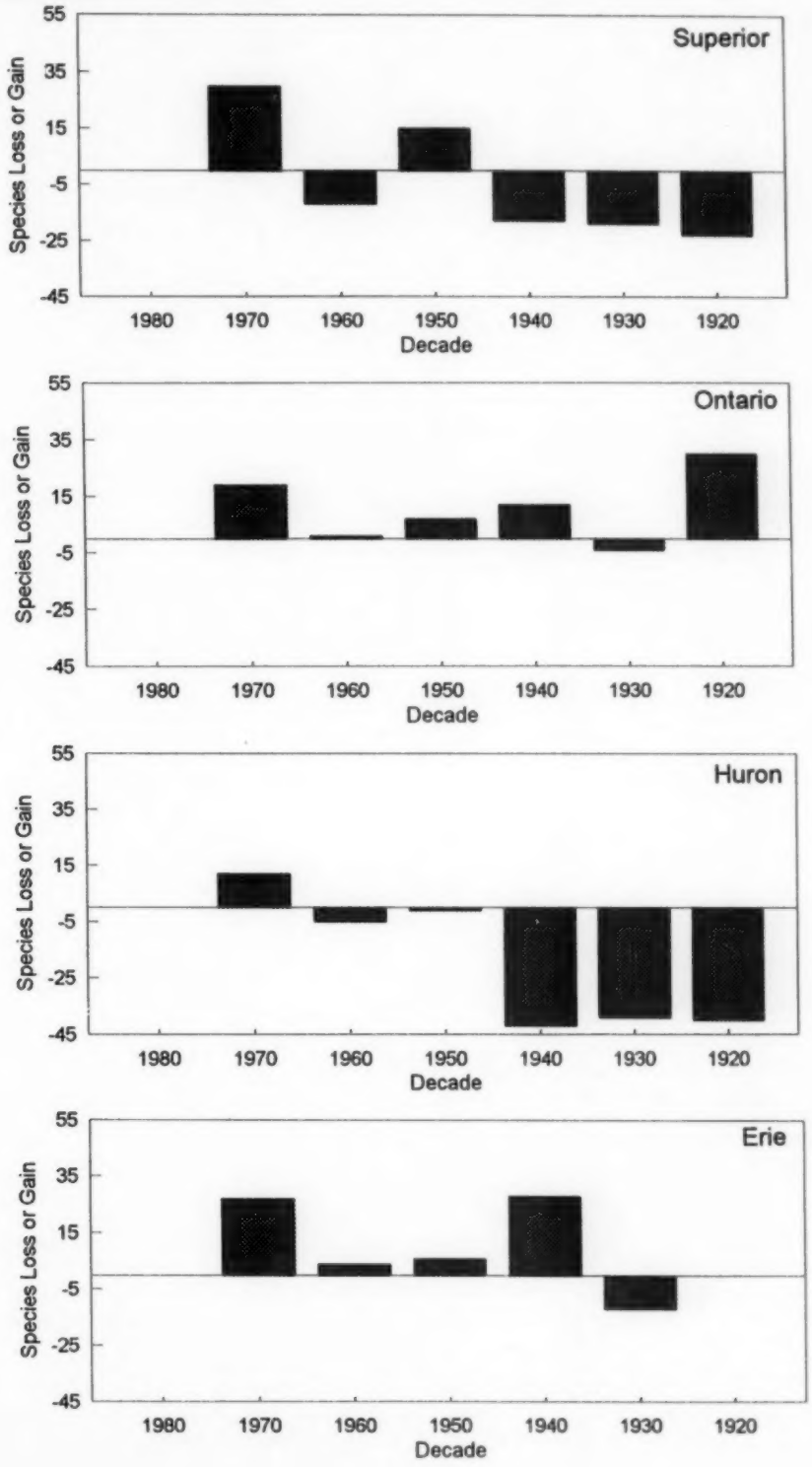

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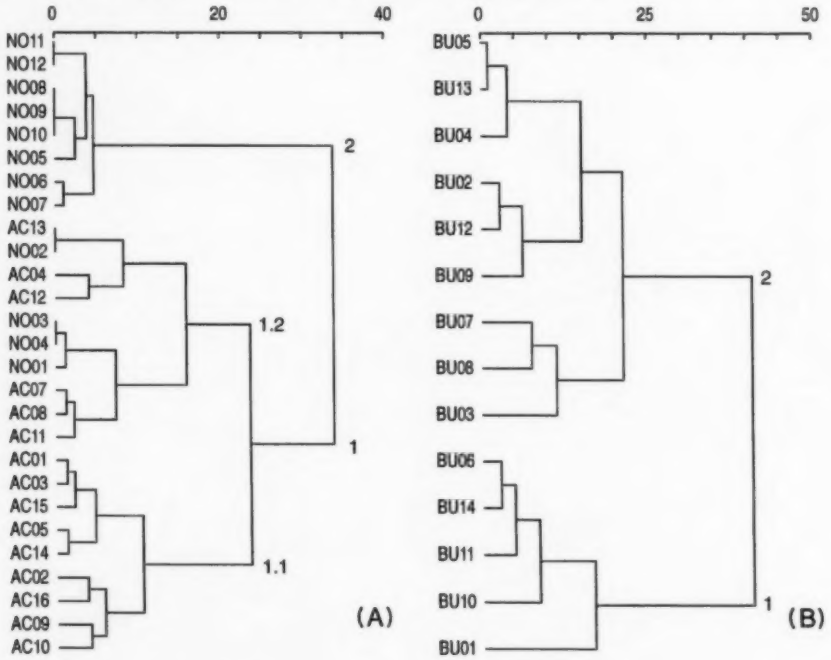
Table 9. Cross-tabulation of the fish species cluster obtained here (Table 8, all species at all sites) with the regional affinities of indigenous species reported by Mandrak and Crossman (1992) (MC).

	MC regional groupings							
Species clusters	Ubiquitous	Great Lakes and Nelson R	Southern Ontario	Southwestern Ontario	Eastern Ontario	Misc.	Unknown	Non-indigenous
1.1	8	3	2	2	0	0	1	1
1.2.1	11	0	0	0	0	1	0	3
1.2.2	8	1	2	1	1	0	2	0
2.1.1	3	5	4	0	0	0	0	2
2.1.2	2	9	5	0	0	1	0	0
2.2	1	3	3	11	3	4	5	3
Total	33	21	16	14	4	6	8	9

Fig. 7. Cluster dendrograms of (A) sites and (B) impaired beneficial uses based on the presence–absence of impairments ($N = 14$) at all AOC and non-AOC sites ($N = 27$). The cluster numbers correspond to those given in Table 10.



bled (Fig. 7A). The clustering of uses produced two groups which did not meet the significance criterion, $P = 0.032$ (Fig. 7B). However, inspection of the reordered binary matrix showed that the Lake Superior non-AOCs largely grouped with the AOCs because of the absence of a number of the five use impairments in group 1: consumption advisories (BU01), degradation of benthos and aesthetics (BU06 and BU11), beach closings (BU10), and loss of habitat (BU14).

At the AOCs, the presence–absence matrices for major contaminants, contaminant sources, and contaminants in fishes reveal patterns among sites (Tables 11, 12, and 13). Copper, iron, nickel, polychlorinated biphenols (PCBs), and fecal coliform exceedances were reported at all AOCs (Table 11). Other metals were reported at most sites. Cluster analysis of major contaminants did not produce a significant clustering of AOCs but two groupings of contaminants were close to being significant, $P = 0.038$ (Table 10). The smaller cluster (marked by asterisks in Table 11) linked arsenic, polyaromatic hydrocarbons (PAHs), phenols, resin and fatty acids, aluminum, selenium, silver, mirex, and cyanide, contaminants that have the lowest reporting in the data set, and hence their grouping is likely spurious.

Among contaminant sources, sewage treatment plants were reported as problems at all AOCs (Table 12). Combined sewer overflows and storm sewer outfalls were more prevalent as of concern in the lower Great Lakes where urbanization is more extensive. Cluster analysis produced two groups of sites that were almost significant ($P = 0.020$; Table 10). The separation of AOCs into groups was largely determined by the absence of problem sources grouped in the first of the final cluster groupings of sources, especially petrochemical and chemical industries, and industrial waste disposal sites.

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Table 10. Site and ecosystem attribute clusters in the binary matrices of the attribute presence–absence data at AOCs and non-AOCs for impaired beneficial uses, major contaminants, contaminant sources, and contaminants and their sources combined.

Data set and analysis	χ^2	P	Cluster No.	No. of members	Description or listing of cluster membership
Impaired beneficial uses					See Fig. 8
27 sites	33.74	0.001	1	19	All AOCs + Non-AOCs 1–4
			2	8	Non-AOCs 5–12
14 uses	40.87	0.032	1	5	Nos. 1, 6, 10, 11, 14
			2	9	Nos. 2–5, 7–8, 12, 13
Major contaminants (Table 11)					
15 AOCs	27.38	0.287	—	—	—
25 contaminents	24.67	0.038	1	16	All without * in Table 11
			2	9	Those marked with * in Table 11
Contaminant sources (Table 12)					
15 AOCs	22.65	0.020	1		Nos. 1, 9–10, 12, 15–16
			2		Nos. 2–8, 11, 13
12 sources	21.65	0.086	1	8	All others
			2	4	Pulp and paper
All contaminants and sources					
15 AOCs	54.62	0.076	1	12	AOCs 1–8, 11, 13–15
			2	3	AOCs 9, 10, 12
42 contaminents	46.42	0.001	1	27	See dendrogram (Fig. 7)
			2	15	See dendrogram (Fig. 7)
	31.07	0.005	1.1	20	See dendrogram (Fig. 7)
			1.2	7	See dendrogram (Fig. 7)
			1.1.1	17	See dendrogram (Fig. 7)
			1.1.2	3	See dendrogram (Fig. 7)

Table 11. List of major contaminants reported to be present at significant levels in water or sediments at the Great Lakes' Areas of Concern included in this study.

	Area of Concern														
Contaminant	1	2	3	4	5	7	8	9	10	11	12	13	14	15	16
Lead	✓	—	—	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Mercury	✓	✓	✓	✓	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	✓
Zinc	✓	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Copper	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Arsenic*	✓	—	—	—	✓	—	—	—	✓	--	✓	✓	—	✓	✓
Iron	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Nickel	✓	✓	✓	✓	3	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chromium	✓	✓	✓	✓	✓	✓	—	✓	✓	✓	✓	—	✓	✓	✓
Aluminum*	✓	—	—	✓	—	✓	—	—	—	✓	✓	—	—	—	—
Selenium*	—	—	—	—	—	—	—	—	—	—	✓	—	—	—	—
Silver*	—	—	—	—	—	—	—	—	—	—	✓	—	—	—	—
Cadmium	✓	✓	✓	—	✓	—	—	✓	✓	—	✓	✓	✓	✓	✓
Phenols*	✓	✓	✓	✓	✓	—	—	—	—	—	✓	—	—	✓	✓
Cyanide*	—	—	—	—	—	—	—	—	✓	—	✓	—	—	—	—
PCBs	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Mirex*	—	—	—	—	—	—	—	—	—	—	✓	—	—	—	—
PAHs*	✓	—	—	—	✓	—	—	—	—	—	✓	✓	—	—	✓
N2 forms	✓	—	✓	—	✓	—	—	✓	—	✓	✓	✓	✓	—	✓
Phosphorus	✓	—	✓	—	✓	✓	✓	—	✓	✓	—	✓	✓	✓	✓
Algae	—	✓	—	—	✓	✓	✓	—	—	—	—	✓	✓	✓	✓
Impaired oxygen	✓	—	—	—	—	✓	—	—	—	✓	—	✓	—	✓	—
Suspended solids	—	—	—	—	—	—	—	—	—	✓	—	✓	✓	✓	—
Oil and grease	✓	—	✓	✓	✓	—	✓	✓	✓	—	—	✓	✓	—	✓
Resin and fatty acids*	✓	✓	✓	✓	—	—	—	—	—	—	—	—	—	—	—
Fecal coliform bacteria	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

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Table 12. List of contaminant sources reported in the Great Lakes' Areas of Concern included in this study.

	Area of Concern														
Source	1	2	3	4	5	7	8	9	10	11	12	13	14	15	16
Petrochemical industries	—	—	—	—	—	—	—	✓	3	—	✓	—	—	—	—
Pulp and paper industries	✓	✓	✓	✓	✓	—	—	✓	—	—	✓	—	—	✓	✓
Steel mills	—	—	—	—	✓	—	—	—	✓	—	✓	✓	—	—	—
Chemical companies	✓	—	—	—	—	—	—	✓	✓	—	✓	—	—	✓	✓
Canneries	—	—	—	—	—	—	—	—	—	✓	—	—	—	—	—
Fish processing plants	—	—	—	—	—	—	—	—	—	✓	—	—	—	—	—
Distilleries	—	—	—	—	—	—	✓	—	✓	—	—	—	—	✓	—
Wood preservative operations	✓	—	—	—	—	—	—	—	—	—	—	—	—	✓	—
Sewage treatment plants	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Combined sewer overflows	—	—	—	—	✓	—	✓	✓	✓	—	✓	✓	✓	✓	✓
Storm sewer outfalls	—	—	—	✓	✓	—	✓	✓	✓	—	✓	✓	✓	✓	—
Industrial waste disposal sites	—	—	—	—	—	—	—	✓	✓	—	✓	—	—	✓	—

Table 13. List of contaminants whose levels in fish invoke consumption advisories in the Great Lakes' Areas of Concern included in this study.

	Area of Concern														
Contaminant	1	2	3	4	5	7	8	9	10	11	12	13	14	15	16
Mercury	✓	✓	✓	✓	✓	—	✓	✓	✓	—		✓	✓	—	✓
Lead	—	—	—	—	—	—	—	✓	—	—	—	—	—	—	—
Mirex	—	—	—	—	—	—	—	—	—	—	✓	✓	✓	✓	—
PCBs	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
DDT	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dioxins	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Furans	—	—	—	—	—	—	—	—	—	—	✓	—	—	—	—

The fish contaminant data set showed that PCBs and mercury levels in fish exceeded consumption advisory levels at many sites (Table 13). These data were not clustered as so few chemicals were involved.

Finally, the major contaminant, contaminant source, and fish contaminant data sets were combined in a single cluster analysis after deletion of dioxins and DDT in fish as these body burdens were absent in fish at all AOCs. The site clustering produced two groups and these were not significant ($P = 0.076$; Table 10). However, three sites on connecting channels (St. Clair, Detroit, and Niagara rivers) formed the second cluster and their grouping was largely attributable to the presence of petrochemical and chemical industries, and industrial waste chemical sites. The combined contaminants clustering produced three significant groups at $P < 0.001$ and $P = 0.005$ and a fourth grouping was close to significance ($P = 0.066$; Table 10). The dendrogram of contaminants shows linkages of major contaminants, sources, and fish contaminants (Fig. 8). Group 2 joins the chemical industries with steel, distilleries, and sewer overflows and storm outfalls; group 1.1 links group 1.1.1, sewage treatment plants, with group 1.1.2, pulp and paper operations. The linkages between sources and contaminants are not immediately obvious.

The cluster analyses of ecosystem perturbations at AOCs and other sites produce groupings that differ from those groupings obtained by clustering fish species presence–absence data. This difference indicates that site-specific perturbations are probably not responsible for the lake and regional associations observed with the fish presence–absence data.

Discussion

The results presented here indicate that fish species measurements at a location in the Great Lakes is primarily related to a response to regional factors. At the level of our analysis, grouping of site characteristics did not relate to grouping of fish species assemblages occurring at these sites. As a consequence, fish species assemblages at AOCs approximate those of non-AOC sites. Because these results imply that fisheries restoration can most effectively be accomplished by management action at regional, as opposed to local, scales it is appropriate to evaluate the factors most likely to affect our conclusion.

First, fish species lists derived for Great Lakes sites may be incomplete or unreliable. Bowlby and Green (1987) showed that fish species lists from Ontario lake inventories were incomplete. Minns (1989) indicated that repeated assessment was required to ensure completeness of taxocene lists. The difference between the species list from electrofishing at AOC sites and from the Fish Species Distribution Data System (Table 7) indicates that (1) the electrofishing assessment was probably inadequate and that repeated surveys would be desirable, (2) the bias of the electrofishing technique or the use of only one sampling method may have reduced the length of species lists for each site, and (3) the Fish Species Distribution Data System, which used a variety of sampling techniques and accumulates data through time may provide more complete and valuable species lists. Consequently, our and other regional analyses of species richness and the factors that affect

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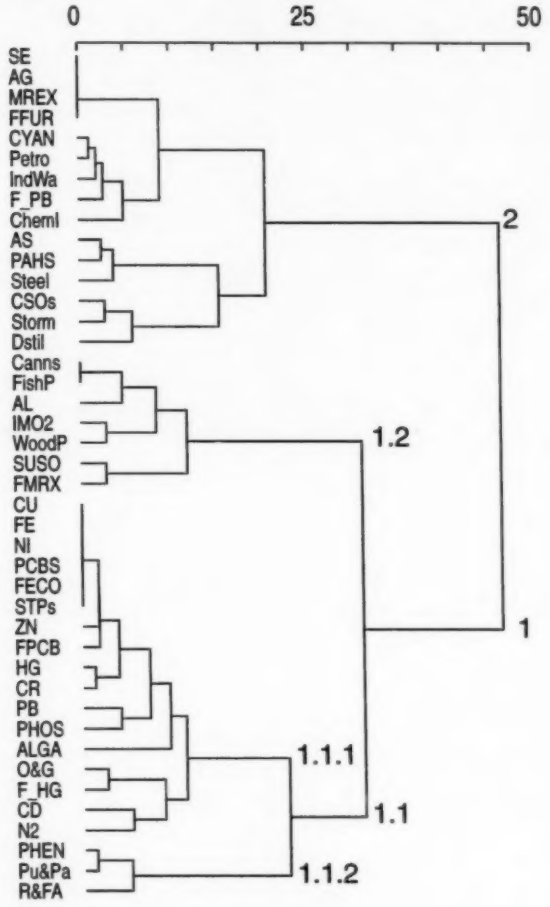
Fig. 8. Cluster dendrogram of combined contaminant criteria (exceedance levels, sources, advisory levels in fish) ($N = 42$) at all AOCs ($N = 15$). The cluster numbers correspond to those given in Table 10.



community structure (Rago and Weiner 1986; Minns 1989; Mandrak and Crossman 1992*b* and others) will be similarly affected by data quality.

The cross-tabulation of Great Lakes fish presence–absence with the regional analysis of postglacial dispersal of freshwater fishes by Mandrak and Crossman (1992*b*) partly led to our inference that regional factors predominate in determining Great Lakes fish species assemblages. Mandrak and Crossman (1992*b*) also used data from the Fish Species Distribution Data System. However, our analysis of independent and combined data sets also produces the same inference, namely, that species assemblages were not directly attributable to site specific characteristics in the Great Lakes. Methodological factors created differences between our data sets for AOCs, and it will only be through increased rigour in future Great Lakes data collection that current inadequacies can be overcome. In the meantime, we conclude that methodological effects combine in an unknown manner with regional factors that influence community structure in the Great Lakes.

Second, our simplification of habitat and chemical characteristics of sites may not adequately represent the local and anthropogenic factors that affect fish species assemblages in the Great Lakes. Data were developed independently at each AOC and both methods and interpretation of level of impairment will differ among sites. Data were sparse for non-AOC sites. It may also be that the level of impairment or the amount of contaminant is more important in determining community structure than simple presence of contamination. However, clear differences in habitat and chemical characteristics occurred and contributed to site groupings. With the data available within the Great Lakes, we were unable to detect site characteristics or site groupings that related to grouping of sites by fish species with few exceptions. There was a difference in number and type of impairment between AOC and non-AOC sites, and there were also significant groupings of AOC sites by type of contaminant and source of contamination. The difference in characteristics of AOC and non-AOC sites may, in fact, be superficial in part because any classification of impairment is a function of availability of data and in part because we are unable to distinguish local differences in fish community structure. However, none of these differences among sites appeared to relate to differences apparent in the fish species community. We, therefore, infer that localized remediation of contamination and habitat degradation are unlikely to produce measurable changes in fish species richness in the Great Lakes.

Third, the site groupings based on fish species assemblages were largely attributed to species differences between the upper and lower Great Lakes and were not created by the species commonly targeted (coregonines, salmonines, percids) for restoration or enhancement. At least three points of view exist by which this result should be judged or used. First, the species targeted for restoration and enhancement are ubiquitous today and occurred historically throughout the Great Lakes; therefore, these species will be present in the Fish Species Distribution Data System, which cumulates data over time and will not contribute to site groupings. However, the electrofishing survey data, the shortest species list, did not cluster differently from the Fish Species Distribution Data System, indicating that these commonly targeted species are still present, and it may be the matter of their abundance that is at issue in management strategies. Second, should initiatives be directed at ecosystem rather than species restoration, the site differences based on presence–absence of species not commonly targeted for restoration and enhancement should play an important role in affecting management initiatives. In other words, the diversity in the community and its species proportions become targets for remediation rather than the abundance of a species. Third, it may be that the species contributing to site groupings are those most affected by site characteristics. Some cyprinids and other species with short life-spans have been promulgated as indicators of anthropogenic stress (Schindler 1987). It may be that, for ecosystem restoration, species not targeted by commercial or sport fishers are most appropriate to gauge success in restoration, and it is biological community properties, not abundance of target species, that form an achievable objective for remedial actions.

Eadie and Keast (1984) and Mandrak (1995) concluded that fish species diversity in Ontario lakes was a result of habitat and prey heterogeneity. That habitat provides the template

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upon which evolution forges species traits and community properties is further supported by arguments of Townsend and Hildrew (1994). At the community level and in the Great Lakes, patchiness in habitat and resources critical to different life stages will be particularly important. Those species that are widely distributed (e.g., coregonines and salmonines) are likely able to take advantage of dispersed or important habitat and will tend to be ubiquitous although their abundance will vary locally. Wide-ranging and diadromous species (McDowall 1996) thus are less likely to contribute to differences in community observed among locations. Conversely, species that are less mobile and more affected by localized changes in resource heterogeneity will contribute to differences in community structure because they are less able to adapt. If these arguments are reasonable, restoration at AOCs may affect local fish community structure but will fail to contribute to species targeted for restoration to enhance opportunity for commercial and sport fishers.

Of the four factors influencing species richness, Minns (1989) suggested that, among Ontario lakes, local factors will dominate regional influences in determining species richness. In the Great Lakes, it seems that if a species is wide ranging or opportunistic, as in the case of many invading species, it will contribute little to differences in local richness or community structure. As a consequence, actions to remediate fish community structure at local levels will be problematic. The relationships among geographic and climatic regional influences, habitat and prey localization, anthropogenic stresses, and biological diversity are imperfectly understood (Myers and Giller 1990; Holdgate 1994). More analysis of the interrelationships and better data collection strategies are critical if efforts devoted to restoration are to produce beneficial resource consequences, to aid us in developing restoration and conservation policies essential to ecosystem sustainability, or to be evaluated. Further, differences in habitat or anthropogenic influence among sites does not appear to result in detectable differences in fish community structure at least in the Great Lakes.

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Nicole Thompson and William Gardner located and organized the data base with which we worked. The Ontario Ministry of Natural Resources was, as usual, generous with their data and help.

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Appendix 1. Complete listing of all fish species by site and data source, including OMNR species codes, common name, and scientific name and the regional group designation.

Code	Common name	Scientific name	Presence–absence by site[a] -AOCs -Non-AOCs -000000001111111-000000000111 -123457890123456-123456789012	MC group[b]
S011	American brook lamprey	*Lampetra appendix*	-000020000000220-202200000002	4SONT
S012	Northern brook lamprey	*Ichthyomyzon fossor*	-2000000000000000-0000000000000	7MISC
S013	Silver lamprey	*Ichthyomyzon unicuspis*	-200002200000002-002000002000	3GLNE
S014	Sea lamprey	*Petromyzon marinus*	-220000000020220-022200002002	0UNKN
S031	Lake sturgeon	*Acipenser fulvescens*	-0000000000000020-2002000000000	2UBIQ
S041	Longnose gar	*Lepisosteus osseus*	-0000231300000232-0000200002000	4SONT
S051	Bowfin	*Amia calva*	-000021131222132-0000000000000	4SONT
S061	Alewife	*Alosa pseudoharengus*	-111023011121331-2000200002020	NONI
S063	Gizzard shad	*Dorosoma cepedianum*	-000021113131330-2000002022200	4SONT
S071	Pink salmon	*Oncorhynchus gorbuscha*	-0220000000000000-2020000000000	NONI
S073	Coho salmon	*Oncorhynchus kisutch*	-0002000000020200-0220000000000	NONI
S075	Chinook salmon	*Oncorhynchus tshawytscha*	-0101130100011100-0020020000000	NONI
S076	Rainbow trout	*Onchorhynchus mykiss*	-331233330001320-2222022020000	NONI
S078	Brown trout	*Salmo trutta*	-0000100300013O1-0000022000000	NONI
S080	Brook trout	*Salvelinus fontinalis*	-2222222000000020-2220022000000	2UBIQ
S081	Lake trout	*Salvelinus namaycush*	-0102000000011320-0000000000000	2UBIQ
S082	Splake	*S. fontinalis* × *S. namaycush*	-0000002000000000-0000220000000	0UNKN
S091	Lake whitefish	*Coregonus clupeaformis*	-133130000000120-2000200200000	2UBIQ
S093	Cisco (lake herring)	*Coregonus artedii*	-2222020000020200-0000000022220	2UBIQ
S094	Bloater	*Coregonus hoyi*	-0000000000000020-0000000000000	0UNKN
S096	Kiyi	*Coregonus kiyi*	-0000000000020020-0000000000000	0UNKN
S102	Round whitefish	*Prosopium cylindraceum*	-3100100000000220-0000000000000	2UBIQ
S121	Rainbow smelt	*Osmerus mordax*	-3331301310233331-0000220020000	6EONT
S131	Northern pike	*Esox lucius*	-3222331330223333-2002200200000	2UBIQ
S132	Muskellunge	*Esox masquinongy*	-0000000002200000-0000200200002	3GLNE
S133	Grass pickerel	*Esox americanus vermiculatus*	-0000000000020020-0000000000000	4SONT
S141	Central mudminnow	*Umbra limi*	-1000223200222230-0022020000200	3GLNE
S152	Mooneye	*Hiodon tergisus*	-0000000000000020-0000000000000	7MISC
S161	Quillback	*Carpiodes cyprinus*	-0000000000020002-2000000220000	3GLNE
S162	Longnose sucker	*Catostomus catostomus*	-3333300000002000-0200020000000	2UBIQ
S163	White sucker	*Catostomus commersoni*	-3333333310333333-2202222222222	2UBIQ
S165	Northern hog sucker	*Hypentelium nigricans*	-0000000200202000-0000220000200	5SWON
S166	Bigmouth buffalo	*Ictiobus cyprinellus*	-0000000000000020-0000000000000	0UNKN
S167	Spotted sucker	*Minytrema melanops*	-0000000020000000-0000000000000	5SWON
S168	Silver redhorse	*Moxostoma anisurum*	-1000030010000200-0000000000200	2UBIQ
S170	Golden redhorse	*Moxostoma erythrurum*	-0000000000020000-0000000000000	5SWON
S171	Shorthead redhorse	*Moxostoma macrolepidotum*	-1100011110310300-0000000000000	2UBIQ
S172	Greater redhorse	*Moxostoma valenciennesi*	-0000000200200200-0000000000000	4SONT
S181	Goldfish	*Carassius auratus*	-0000000011333000-0000000000000	NONI
S182	Northern redbelly dace	*Phoxinus eos*	-2200002000002200-0000000000000	2UBIQ
S183	Finescale dace	*Phoxinus neogaeus*	-2020002000000200-0000022000000	2UBIQ
S184	Redside dace	*Clinostomus elongatus*	-0000000000000200-2020020000202	5SWON
S185	Lake chub	*Couesius plumbeus*	-3312102000002000-2220020000000	2UBIQ
S186	Carp	*Cyprinus carpio*	-3310133331333330-0020000220200	NONI
S189	Brassy minnow	*Hybognathus hankinsoni*	-0000002000002200-0000022222000	3GLNE
S192	Hornyhead chub	*Nocomis biguttatus*	-0000020220200000-0000000000000	5SWON
S193	River chub	*Nocomis micropogon*	-0000000000020200-0000000000000	5SWON
S194	Golden shiner	*Notemigonus crysoleucas*	-0000130130333330-0002022022000	3GLNE
S196	Emerald shiner	*Notropis atherinoides*	-3300123331313300-0220020222200	2UBIQ
S197	Bridle shiner	*Notropis bifrenatus*	-0000000000000020-0000000000000	6EONT
S198	Common shiner	*Luxilis cornutus*	-0000333300233320-0002022222200	2UBIQ
S199	Blackchin shiner	*Notropis heterodon*	-0000002200020200-0000220000000	3GLNE

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Appendix 1 *(continued).*

Code	Common name	Scientific name	Presence–absence by site[a] -AOCs -Non-AOCs -000000001111111-000000000111 -123457890123456-123456789012	MC group[b]
S200	Blacknose shiner	*Notropis heterolepis*	-020000002022222-200220000000	2UBIQ
S201	Spottail shiner	*Notropis hudsonius*	-333213131031333-022022002220	2UBIQ
S202	Rosyface shiner	*Notropis rubellus*	-000000020000220-002200002022	4SONT
S203	Spotfin shiner	*Cyprinella spiloptera*	-000000022022222-000000022200	4SONT
S204	Sand shiner	*Notropis stramineus*	-000012320022302-000000002002	4SONT
S205	Redfin shiner	*Lythurus umbratilis*	-000000020000000-000000000000	5SWON
S206	Mimic shiner	*Notropis volucellus*	-000033332020022-000020022000	3GLNE
S207	Pugnose minnow	*Opsopoedus emiliae*	-000000002000000-000000000000	5SWON
S208	Bluntnose minnow	*Pimephales notatus*	-000033333033323-000020222202	3GLNE
S209	Fathead minnow	*Pimephales promelas*	-300000220023320-000000022200	2UBIQ
S210	Blacknose dace	*Rhinichthys atratulus*	-200022220002220-202002222222	3GLNE
S211	Longnose dace	*Rhinichthys cataractae*	-202220200022220-222202202022	2UBIQ
S212	Creek chub	*Semotilus atromaculatus*	-200022220022220-002022222222	2UBIQ
S213	Fallfish	*Semotilus corporalis*	-000000020000020-000000000000	7MISC
S214	Pearl dace	*Margariscus margarita*	-200000200002020-000002002220	2UBIQ
S217	Striped shiner	*Luxilis chrysocephalus*	-000002020020000-000000000000	5SWON
S218	Ghost shiner	*Notropis buchanani*	-000000200000000-000000000000	0UNKN
S231	Black bullhead	*Ameiurus melas*	-000000020020000-000000000000	5SWON
S232	Yellow bullhead	*Ameiurus natalis*	-000000022020002-000000000000	4SONT
S233	Brown bullhead	*Ameiurus nebulosus*	-000023101123333-002020002000	3GLNE
S234	Channel catfish	*Ictalurus punctatus*	-000000020020020-000000022200	4SONT
S235	Stonecat	*Noturus flavus*	-000000000200220-000000020220	4SONT
S236	Tadpole madtom	*Noturus gyrinus*	-000002020022200-000000000000	3GLNE
S237	Brindled madtom	*Noturus miurus*	-000000000020000-000000000000	5SWON
S251	American eel	*Anguilla rostrata*	-200000000211331-000000000000	6EONT
S261	Banded killifish	*Fundulus diaphanus*	-000002200022222-000022000000	4SONT
S271	Burbot	*Lota lota*	-313110001000220-200222200000	2UBIQ
S281	Brook stickleback	*Culaea inconstans*	-312030020002220-222002222222	2UBIQ
S282	Threespine stickleback	*Gasterosteus aculeatus*	-000000000020222-000000000000	7MISC
S283	Ninespine stickleback	*Pungitius pungitius*	-333010000000020-000000000000	2UBIQ
S291	Trout-perch	*Percopsis omiscomaycus*	-333210111021320-222200022000	2UBIQ
S301	White perch	*Morone americana*	-000000011133330-000000000000	NONI
S302	White bass	*Morone chrysops*	-000022001120330-000000022000	4SONT
S311	Rock bass	*Ambloplites rupestris*	-300033333031333-000222220222	3GLNE
S312	Green sunfish	*Lepomis cyanellus*	-000000022200000-000000000000	3GLNE
S313	Pumpkinseed	*Lepomis gibbosus*	-000033133123333-000022022222	3GLNE
S314	Bluegill	*Lepomis macrochirus*	-000000033101232-000002020200	3GLNE
S315	Longear sunfish	*Lepomis megalotis*	-000000020000000-000000000000	3GLNE
S316	Smallmouth bass	*Micropterus dolomieu*	-100033311031132-000222222220	3GLNE
S317	Largemouth bass	*Micropterus salmoides*	-000013031133333-000022022200	3GLNE
S318	White crappie	*Pomoxis annularis*	-000000020022002-000000000000	5SWON
S319	Black crappie	*Pomoxis nigromaculatus*	-000023033123333-200020022200	3GLNE
S331	Yellow perch	*Perca flavescens*	-333233133033333-220222222200	2UBIQ
S332	Sauger	*Stizostedion canadense*	-020022000000000-000000000000	2UBIQ
S333	Blue pike	*Stizostedion vitreum glaucum*	-000000000000020-000000000000	0UNKN
S334	Walleye	*Stizostedion vitreum vitreum*	-322033133230031-200020022000	2UBIQ
S337	Rainbow darter	*Etheostoma caeruleum*	-000000200020220-000000002022	5SWON
S338	Iowa darter	*Etheostoma exile*	-020002020020220-000022200000	2UBIQ
S339	Fantail darter	*Etheostoma flabellare*	-000000000020220-000000000000	0UNKN
S340	Least darter	*Etheostoma microperca*	-000000020000020-000000000000	5SWON
S341	Johnny darter	*Etheostoma nigrum*	-330033232022332-202222222200	2UBIQ
S342	Logperch	*Percina caprodes*	-332213033032233-020220002000	2UBIQ
S344	Blackside darter	*Percina maculata*	-000000002020000-000000002200	3GLNE

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Appendix 1 *(concluded).*

Code	Common name	Scientific name	Presence–absence by site[a] -AOCs -Non-AOCs -000000001111111-000000000111 -123457890123456-123456789012	MC group[b]
S346	Tessellated darter	*Etheostoma olmstedi*	-000000000020222-000000000000	6EONT
S361	Brook silverside	*Labidesthes sicculus*	-000003031001020-000020002200	4SONT
S371	Freshwater drum	*Aplodinotus grunniens*	-000000031131130-000000022200	7MISC
S381	Mottled sculpin	*Cottus bairdi*	-331132230020320-222202200000	2UBIQ
S382	Slimy sculpin	*Cottus cognatus*	-111330200000320-000000000000	2UBIQ
S384	Deepwater sculpin	*Myoxocephalus thompsoni*	-000000000020000-000000000000	7MISC

[a] 0, absent; <0, present; 1, electrofishing; 2, Ministry, 3, both.

[b] MC groups are given in Mandrak and Crossman (1992); NONI, non-indigenous; 0UNKN, biogeographic group unknown.

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Historical land use, phosphorus loading, and loss of fish habitat in Lake Simcoe, Canada

David O. Evans, Kenneth H. Nicholls, Yvonne C. Allen, and Michael J. McMurtry

Abstract: Our purpose was to develop a case study linking human land-use activities, phosphorus (P) loading, hypolimnetic dissolved oxygen depletion, and loss of cold-water fish habitat in Lake Simcoe, Canada. Conversion from forested to agricultural land began during the 1820s and was largely completed by 1890. Erosional P inputs to Lake Simcoe sediments increased from pre-agricultural loads of about 30–100 $t \cdot yr^{-1}$ by the 1940s. Point-source loads of P first appeared about 1910, remained low at 2–3 $t \cdot yr^{-1}$ until the 1960s, then increased to about 20 $t \cdot yr^{-1}$ by 1990, as human population in the basin increased from about 50 000 to > 250 000 residents. Recruitment failure of lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and lake herring (*Coregonus artedii*), occurred during the 1960s, 1970s, and 1980s, respectively, as hypolimnetic water quality deteriorated. The volume-weighted, temperature-corrected hypolimnetic dissolved oxygen concentration from August 30 to September 19 declined from about 4.5 $mg \cdot L^{-1}$ in 1975 to 2.0 $mg \cdot L^{-1}$ by 1993. During late summer, 1975–1993, 60–98% of the 6–12°C thermal habitat volume had < 7 $mg \cdot L^{-1}$ dissolved oxygen, and 10–50% had < 3 $mg \cdot L^{-1}$, the incipient lethal threshold for lake trout. Reduction of P loads to surface waters and restoration of cold-water fish habitat are now the explicit management goals of the Lake Simcoe Environmental Management Strategy.

Résumé : Nous avions pour objectif une étude de cas faisant le lien entre l'utilisation humaine du territoire, la charge en phosphore, l'épuisement de l'oxygène dissous dans l'hypolimnion et la perte d'habitat du poisson d'eau froide dans le lac Simcoe au Canada. Le déboisement à des fins agricoles s'est amorcé dans les années 1820 et il était pratiquement achevé en 1890. La charge en phosphore mesurée dans les sédiments du lac Simcoe, et associée à l'érosion, s'est accrue pour passer de 30 $t \cdot an^{-1}$ à 100 $t \cdot an^{-1}$ dans les années 1940. Les charges en phosphore d'origine ponctuelle sont apparues pour la première fois vers 1910 et elles sont restées assez peu importantes, soit à 2–3 $t \cdot an^{-1}$, jusque vers les années 1960, pour ensuite s'élever à environ 20 $t \cdot an^{-1}$ en 1990, tandis que la population dans ce bassin hydrographique s'élevait, passant d'environ 50 000 personnes à plus de 250 000. Le recrutement chez le touladi, le grand corégone et le cisco a co mmencé à marquer un recul dans les années 1960, 1970 et 1980, respectivement, à mesure que la qualité de l'eau de l'hypolimnion se détériorait. La concentration de l'oxygène dissous dans cette couche d'eau, corrigée pour la température et pondérée en fonction du volume, mesurée entre le 30 août et le 19 septembre, est passée d'environ 4,5 $mg \cdot L^{-1}$ en 1975 à 2,0 $mg \cdot L^{-1}$ en 1993. Dans la période allant de 1975 à 1993, vers la fin de l'été, la teneur en oxygène dissous de 60% à 98% du volume de l'habitat, dans la plage de température allant de 6°C à 12°C, était inférieure à 7 $mg \cdot L^{-1}$; elle était inférieure à 3 $mg \cdot L^{-1}$, seuil de létalité du touladi, dans 10% à 50% de ce volume. Le but explicitement fixé pour la Stratégie de gestion écologique du lac Simcoe est de réduire la charge en phosphore dans les eaux de surface et de rétablir l'habitat du poisson d'eau froide.
[Traduit par la Rédaction]

Introduction

The Lake Simcoe basin has been influenced by human development for more than 200 yr (Wilson and Ryan 1988) and subjected to extensive erosion from agricultural activities (Wilson 1989) that, combined with urban development, has resulted in a threefold increase in phosphorus (P) loading from presettlement rates (Johnson and Nicholls 1989). In recent decades, natural recruitment of the native cold-water fishes, lake trout, (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and lake herring (*Coregonus artedii*), has declined (Evans and Waring 1987), and the sustainability of these species is now in question. The possible causes of fish recruitment failure include eutrophication, contaminants, siltation, and exotic species, but the former has been identified as the major concern (Evans et al. 1988; LSEMS 1995). This paper develops a case history of human land use and aquatic ecosystem change in the Lake Simcoe watershed and identifies the processes linking land use and aquatic ecosystem function, with specific reference to P loading, dissolved oxygen and cold-water fish habitat.

We synthesized information from new research findings, published scientific papers and unpublished reports. We focused on the effects of siltation and nutrient loading from land-use activities (agriculture, urban, and recreational development) on cold-water fish species, with emphasis on the hy-

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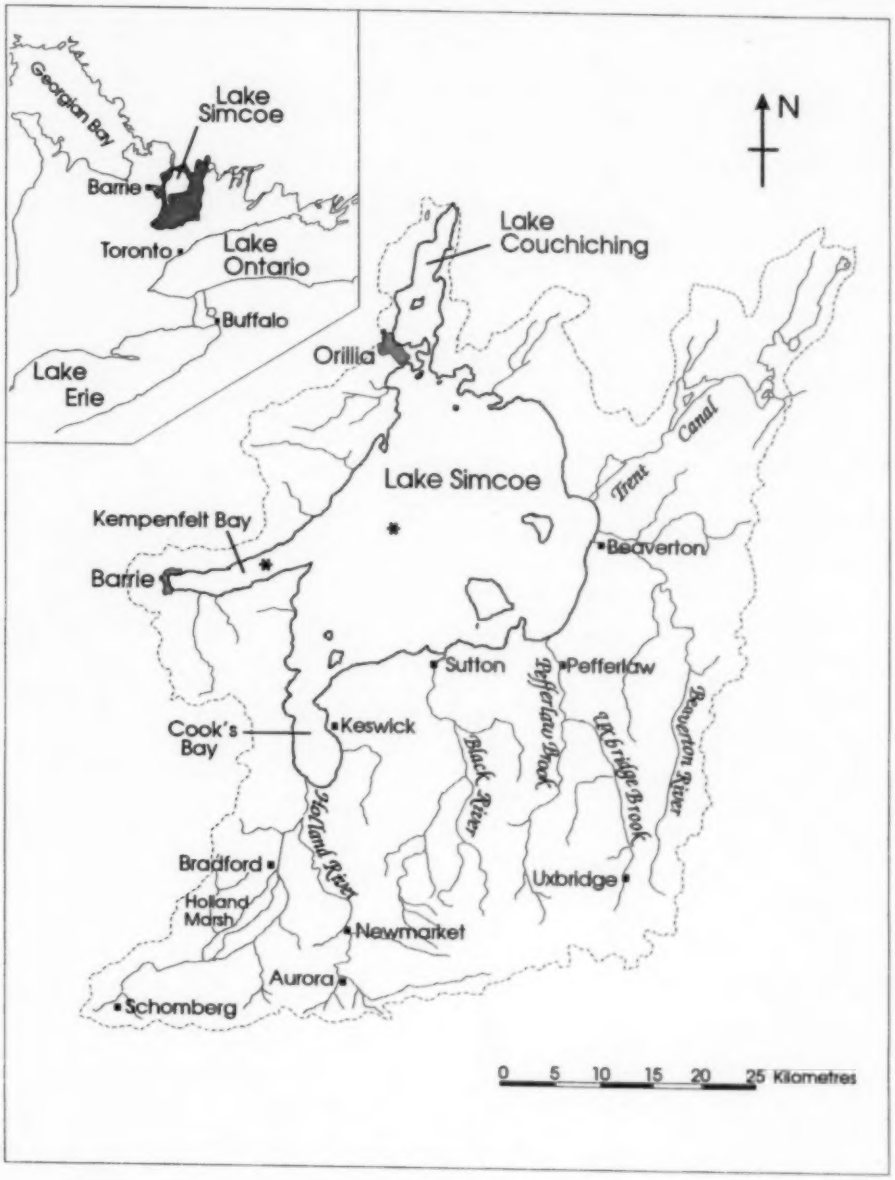
Fig. 1. Map of the Lake Simcoe and Lake Couchiching catchment basin. The insert shows the location of the Lake Simcoe watershed in southern Ontario.



polimnetic summer habitats of the native lake trout, lake whitefish, and lake herring. Our objective was to link land-use to loss of fish habitat through the following known mechanisms: (1) land use and P loads; (2) P load and phytoplankton production; (3) phytoplankton production, decay, and biological oxygen demand; (4) biological oxygen demand and degradation or loss of hypolimnetic fish habitat; and (5) loss of fish habitat and loss of production of key fish species.

Lake Simcoe

Lake Simcoe has a surface area of 722 km^2 and is the fifth largest inland lake in Ontario. The lake has two major basins, the central and Beaverton basins, and two major bays, Kempenfelt and Cook's bays (Fig. 1). The central basin has a maximum depth of 33 m, while the Beaverton basin reaches a maximum of about 20 m. Kempenfelt Bay, which lacks a sill and is contiguous with the central basin, has a maximum depth

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Table 1. Physical, chemical, and morphometric characteristics of Lake Simcoe.

Surface area (km^2)	722
Cook Bay (Roches Point - Stony Point) (km^2)	30
Watershed area (km^2)	3572
Island area (km^2)	18.2
Shoreline area (includes islands) (km)	232
Shoreline development	2.27
Elevation (m)	22
Mean depth (m)	14.2
Maximum depth (m)	41.5 (Kempenfelt Bay)
Volume (m^3)	1.025×10^{10}
Mean annual outflow ($m^3 \cdot s^{-1}$)	32.3
Annual outflow volume (m^3)	1.02×10^9
Flushing time (yr)	10.05
Number of tributaries	35
Transparency (ice-free means 1988–1994) (m)	
Mid-lake	4.8
Kempenfelt Bay	4.6
Cook Bay	3.1
MEI	11.7
Hardness ($mg \cdot L^{-1}$)	140
Alkalinity ($mg \cdot L^{-1}$)	125
Conductivity (μmhos; 25°C)	345
pH	8.3
Total dissolved solids ($mg \cdot L^{-1}$)	199
Total phosphorus (mid-lake mean 1987–1994) ($mg \cdot L^{-1}$)	0.015
Outflow (mean 1987–1994) ($mg \cdot L^{-1}$)	0.010

of 41 m, and is mesotrophic. Cook's Bay, which has a maximum depth of 15 m, is eutrophic, receiving loads of silt and P from the agricultural and urban drainage of the Holland River. The central basin of Lake Simcoe is mesotrophic, Secchi transparency varying from 2.5 to 5.0 m at mid-lake during middle to late summer. The lake water is slightly alkaline (pH 8.3) and has high total dissolved solids (199 $mg \cdot L^{-1}$). Table 1 summarizes the key physical, chemical, and morphometric features of the lake. The major tributary rivers originate in the Oak Ridges moraine, which lies to the south of the lake (Fig. 1). These rivers, the Holland, Black, and Beaverton rivers and Pefferlaw and Uxbridge brooks, account for 61% of the total catchment area (LSEMS 1995).

The Lake Simcoe fish community has 55 species representing 15 families. Cold-, cool-, and warm-water species are present, lake trout, lake whitefish, lake herring, northern pike (*Esox lucius*), yellow perch (*Perca flavescens*), and smallmouth bass (*Micropterus dolomieu*), being the most prominent species in the fisheries. Many other species are abundant, including common white sucker (*Catostomus commersoni*), burbot (*Lota lota*), emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*), brown bullhead (*Ictalurus nebulosus*), trout perch (*Percopsis omiscomaycus*), rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), black crappie (*Pomoxis nigromaculatus*), log perch (*Percina caprodes*), Johnny darter (*Etheostoma nigrum*), and mottled sculpin (*Cottus bairdi*). We evaluated habitat loss of the cold-water species, lake trout, lake whitefish, and lake herring, because their nursery and feeding habitats are especially vulnerable to the effects of siltation and nutrient loading, two of the major stressors affecting the lake.

Invasions by northern pike (1920), common carp (*Cyprinus carpio*) (1896), and rainbow smelt (*Osmerus mordax*) (1961), have strongly influenced the structure of the Lake Simcoe fish community (Evans and Waring 1987; Evans et al. 1988). Other more recent invaders, include black crappie (1987), zebra mussel (*Dreissena polymorpha*) (1993), and spiny water flea (*Bythotrephes cederstroemi*) (1993). The effects of these latter introductions have not yet become clearly manifested in fish community changes.

The fisheries of Lake Simcoe are of major social and economic importance. An estimated 172 000 anglers visited the lake during 1990 (LSEMS 1995). The lake supports the highest angling effort of any inland lake in Ontario accounting for 15% of the total effort. The majority of angling takes place during the winter, 2000–4000 fishing huts operating from January to March each year. Winter angling effort in 1993 was three times the summer effort. The most sought after species in the winter fishery are lake trout, lake whitefish, and yellow perch. Approximately $112 million dollars of income is generated annually by the fishery (LSEMS 1995).

Materials and methods

Historical land use

Land-use activities and have been synthesized from Ralston et al. (1975), Craig (1977), LSEMS (1985, 1995), Wilson (1986, 1989), Wilson and Ryan (1988), and Nicholls (1992, 1995*a*). Land-use activities causing erosion of soil and organic nutrients receive special emphasis as have loadings of these materials to the lake. Johnson and Nicholls (1989) was our primary source for sediment and P loading to the lake.

Wilson (1989) estimated soil loss from agricultural lands in the

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Lake Simcoe basin from 1800 to 1981, using the universal soil loss equation (Wischmeier and Smith 1978). Johnson and Nicholls (1988, 1989) determined sedimentation rates, by mapping four sedimentation basins (Kempenfelt Bay, Cook's Bay, central basin and outlet basin; Fig. 1) using sonar and measurements of physical and chemical characteristics of ^{210}Pb-dated sediment cores from each of the major basins of the lake.

Water-quality monitoring has been conducted at sampling stations in all sectors of Lake Simcoe since the early 1980s by the Ontario Ministry of Environment and Energy (OMEE) (Nicholls 1995*b*). Phosphorus, chloride, conductivity, chlorophyll *a*, and phytoplankton biomass, among other variables, have been measured biweekly at lake stations and the outflow during the ice-free period and at four municipal water intake plants throughout the year.

Aquatic ecosystem trends

Temperature and dissolved oxygen profiles

Vertical temperature and dissolved oxygen profiles were collected by the OMEE and the Ontario Ministry of Natural Resources (OMNR) at biweekly intervals from May to October from 1975 to 1993. We used data from two mid-basin stations at 33 m in the central basin and at 38 m in Kempenfelt Bay. These profiles were used to determine the volume of thermally preferred habitat or thermal habitat volume (THV; Christie and Regier 1988) for lake trout, lake whitefish, lake herring, and rainbow smelt and to establish the location of the thermocline, volume of the hypolimnion, and the volume-weighted temperature and dissolved oxygen concentration of the hypolimnion. The interannual variation in the supply of THV and in dissolved oxygen content of the hypolimnion was also determined. We tested for thermal stability over years and adjusted hypolimnetic dissolved oxygen depletion rates to standard temperature and volume conditions to test for trends in trophic state.

Temperature and dissolved oxygen profiles were determined at two stations in Kempenfelt Bay and the central basin (Fig. 1) for 13 dates each year from June 1 to September 29 (calendar days 152–272, except for leap years), representing twelve, 10-day intervals through the summer growing season. Temperature and dissolved oxygen values were linearly interpolated for each profile to obtain estimates at each 1-m depth from the surface to the lake bottom. Where temperature was not recorded to the maximum station depth, the last recorded temperature was assumed to extend to the lake bottom. Where the dissolved oxygen profile did not extend to the maximum station depth, the rate of oxygen depletion with depth was determined, based on the deepest four observations at 1-m intervals, and this rate was used to extrapolate dissolved oxygen to the lake bottom. Extrapolation was never greater than 5 m and extrapolated dissolved oxygen was not allowed to fall below 0 mg·L^{-1}. If a profile was not available for a specific date, the profile was interpolated based on a weighted average of profiles for the nearest available preceding and following dates.

Determination of the thermocline and hypolimnion

The thermocline was the depth zone defined by a temperature change of > 1°C·m^{-1} (Hutchinson 1957). The thermocline boundaries were the upper and lower edges of this zone rounded up or down, respectively, to the nearest metre. When more than one thermocline was defined additional decision criteria were applied: (1) the thermocline could not occur within 5 m of the surface; (2) the thermocline could not occur within 10% of the maximum depth of the station; (3) if the upper and lower critical depths of two adjacent thermoclines were separated by ≤ 6 m, they were assumed to comprise a single thermocline; and (4) if the separation was > 6 m, the thermocline having the greatest change in temperature was selected. The lower boundary of the thermocline was also the upper boundary of the hypolimnion.

Volume-weighted hypolimnetic temperature and dissolved oxygen

Volume-weighted temperature and dissolved oxygen of the hypolimnion were calculated based on profiles taken at the two stations. The Kempenfelt Bay station was used to characterize the eliptical volume of water projected from a depth of 33 m in Kempenfelt Bay to the lake surface and the conical volume at depths greater > 33 m. The maximum depth of the main basin is 33 m, therefore, we knew that the area at depths > 33 m was entirely contained within Kempenfelt Bay. By using the 33 m depth contour in Kempenfelt Bay, we were able to define a mass of water within the bay that was characterized by the unique thermal profile in that part of the lake. The remaining volume of the lake, including area < 33 m outside the eliptical column in Kempenfelt Bay, was modelled based on the area–depth curve for depths < 33 m and the temperature profile for the central basin.

The volume of the hypolimnion in the main basin and in Kempenfelt Bay was calculated separately by summing the volumes of the 1-m frusta from the upper boundary of the hypolimnion to the bottom of the lake for each water mass. The volume of each frustum was calculated as

$$(1) \qquad V = \frac{h}{3(A_1 + A_2 + (A_1A_2)^{0.5})}$$

where h is the height of frustum (1 m in this case), A_1 is the area at depth 1 (top of frustum), and A_2 is the area at depth 2 (bottom of frustum). The volume-weighted mean hypolimnetic temperature (T_{VW}) was also calculated separately for the main basin and Kempenfelt Bay profiles as

$$(2) \qquad T_{vw} = \Sigma((T_1 + T_2)/2)\,((A_1 + A_2 + (A_1A_2)^{0.5})/3)$$

where T_1 is the temperature at depth 1 for each 1-m stratum, T_2 is the temperature at depth 2 for each 1-m stratum, A_1 is the area at depth 1, and A_2 is the area at depth 2. The volume-weighted temperature for the whole lake was calculated for each date (at 10-day intervals) within each year as the mean of the volume-weighted temperatures for the two stations, weighted by the hypolimnetic volume represented by each station's profile. Volume-weighted hypolimnetic dissolved oxygen was calculated in the same way by substituting dissolved oxygen for T in the above equation.

Hypolimnetic dissolved oxygen depletion rates

Dissolved oxygen depletion rates in the hypolimnion were determined for each year based on least squares regression analysis of volume-weighted, mean hypolimnetic dissolved oxygen concentration versus calendar date from day 152 to day 272. The average temperature of the hypolimnion over years varied from 5.73°C in 1991 to 11.24°C in 1981, but the rates of depletion were not significantly correlated ($P > 0.05$) with average hypolimnetic temperature over the same dates and time period; therefore, rates were not corrected for temperature.

Fish community trends

Winter angling harvest data, which spanned the period 1961–1993, were adjusted to a standard 50-day fishing season to allow interannual comparisons of relative abundance of species. Prominent species in the angling catch included lake trout, lake whitefish, lake herring, and rainbow smelt. Some of these data have been previously reported by Evans and Waring (1987) for the period 1961–1983; the winter harvest of the cold-water fishes has been extended with biannual surveys to 1993.

Fish distribution

The distribution of offshore fishes was investigated during September 1982 and 1983, using multimesh monofilament gill nets. Each gill net consisted of 9–11 panels of monofilament mesh, including 1.27, 1.91, 2.54, 3.81, 5.08, 6.35, 7.62, 8.89, 10.16, 11.43, and 12.70 cm stretched measure. The height of the nets was 2.4 m and each panel

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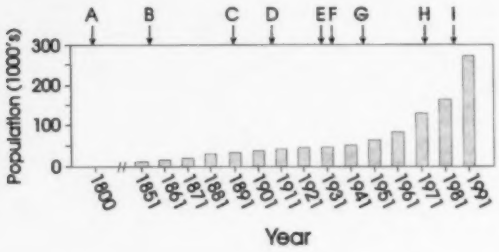
Fig. 2. Changes in the non-indigenous human population in the Lake Simcoe basin since 1800 AD and dates of significant human influence. Dates are indicated by arrows and capital letters: (A) 1794, first farm was established in the basin; (B) 1853, completion of Toronto to Bradford railway line; (C) 1891, 87% of the basin had been converted to farmland; (D) 1907, completion of the Trent Canal; (E) 1927–1930, agricultural development of the Holland Marsh; (F) 1933, the first sewage treatment plant was built; (G) initial use of phosphates in detergents; (H) 1971–1973, implementation of detergent phosphate legislation; (I) 1984, diversion of sewage from Aurora and Newmarket out of the Lake Simcoe basin.



was 15.2 m in length. The nets were set on the lake bottom for 2–4 h during the day (09:00–18:00) at 5, 10, 15, 20, 25, and 30 m along a transect from Sibbald Point to the central basin water sampling station (Fig. 1). Four sets were made within 1 km of the transect intersection point with each depth contour, usually on different days. Catches were corrected to catch-per-unit-effort. Weighted mean depths, temperatures, and dissolved oxygen concentrations at the capture sites were calculated based on individual captures for each species. The purpose of the netting study was to determine depth distribution and habitat use by the offshore fish species during the critical period of late summer thermal and dissolved oxygen stratification.

Calculation of fish habitat volumes

A hypsographic curve for Lake Simcoe was determined by planimetry from chart 2015 (Canadian Hydrographic Service, Department of Fisheries and Oceans, 1980) at a scale of 1 : 63 360. Area at depth was then interpolated from 5-m depth intervals to 1-m intervals. The volume of each 1-m stratum was calculated as in eq. 1.

The habitat volume is the summed volumes between two depths corresponding to bounds such as the preferred thermal ranges of 8–12°C and 10–14°C for lake trout and lake whitefish, respectively. We calculated habitat volumes for temperature and dissolved oxygen criteria as follows: (1) optimal habitat (AHV7), defined as the species bounds for THV and dissolved oxygen > 7 $mg \cdot L^{-1}$, which corresponds with minimal impairment of activity in salmonids (Davis 1975); (2) suboptimal habitat (AHV5), bounded by THV, but with a minimum dissolved oxygen of 5 $mg \cdot L^{-1}$, which causes about a 50% reduction in maximum potential activity levels in lake trout (Gibson and Fry 1954); and (3) critical habitat (AHV3), bounded by THV, but with a minimum dissolved oxygen of 3 $mg \cdot L^{-1}$, which is near the incipient lethal threshold or the level of no excess activity (Fry 1971) for salmonids. Where depth boundaries were intermediate between 1-m strata, the corresponding fraction of the stratum volume was included in the summation. The volume of the hypolimnion was calculated by estimating the volume from the top of the hypolimnion to the lake bottom.

Results

Land-use changes

By 1820, most of the land grants available to settlers on the upper Holland River watershed had been claimed. In 1818, native peoples surrendered all land around Lake Simcoe to the Government of Upper Canada and retreated to reservations on Snake and Georgina Islands and in Rama Township. Settlers from the British Isles and from Europe began clearing the land (which by this time had been organized into townships) on the eastern and western shores of the lake during the 1820s. By 1853, a railway line had been constructed between Toronto and Bradford, which greatly facilitated the transportation of supplies and equipment required for continued urbanization and agriculturalization of the basin (MacCrimmon and Skobe 1970; Craig 1977).

Although most of the conversion from forested land to agriculture occurred during the period 1820–1890, more than 70% of the present-day population accrued during the past 30 years (Fig. 2), as a result of expansion of Barrie, Newmarket, Aurora, Orillia, Bradford, Sutton, Keswick, Uxbridge, and other smaller centres, all of which were well established during the latter part of the 19th century. Over the past three decades, Statistics Canada census data indicate that the human population more than tripled in the Lake Simcoe basin from an estimated 85 300 in 1961 to 271 400 in 1991 (Fig. 2).

Deforestation and agriculture

The consequences of deforestation and agriculturalization have had important water quality and ecological implications for the Lake Simcoe ecosystem. Most notable changes included an increased mass sedimentation rate of soil particles eroded from the watershed and increased loading of P to the lake. Between 1851 and 1891, when the area of farmland nearly doubled from 137 000 to 25 400 ha (Fig. 3), a peak in erosional losses of about 860 000 $t \cdot yr^{-1}$ was calculated by Wilson (1986). Most of these soil losses were from fallow fields and row crops. A general trend to declining soil losses between 1911 and 1961 was related to a trend to higher proportions of the total agricultural area in hay and pasture. Total farmland area remained fairly constant during this time period (Wilson 1986). The area planted to corn increased from 1.4 to 21% of farmland between 1961 and 1981, and was (along with lesser increases in soybeans) responsible for soil losses increasing again through the 1960s and 1970s even though total area in agriculture declined (Fig. 3). The net result of changing crop patterns particularly to corn and soybeans was that soil erosion increased from an historical low of 1.73 $t \cdot ha^{-1}$ in 1961 to 3.12 $t \cdot ha^{-1}$ in 1981 (Wilson 1989).

The thickness of postglacial sediments in the lake ranged from 0 (in shallow nonsedimentation zones) to a maximum of 655 cm in the northern outlet basin. Sedimentation rate averaged about 27 000 $t \cdot yr^{-1}$ presettlement, about 55 000 $t \cdot yr^{-1}$ for the period 1885–1985, and 64 000 $t \cdot yr^{-1}$ for the contemporary (1980s) period (Johnson and Nicholls 1989). Although there were differences among the four sub-basins during postsettlement times, a general agreement with Wilson's temporal model was evident (i.e., peak loading rate in the late 1800s) declines to about 1960 and increases again through the 1960s and 1970s. The decline in area of agricultural land in the Lake Simcoe basin has continued to the present time and is coincident with both reversion of cleared land to forest, wetlands, and scrublands and with accelerating urbanization (Fig. 3).

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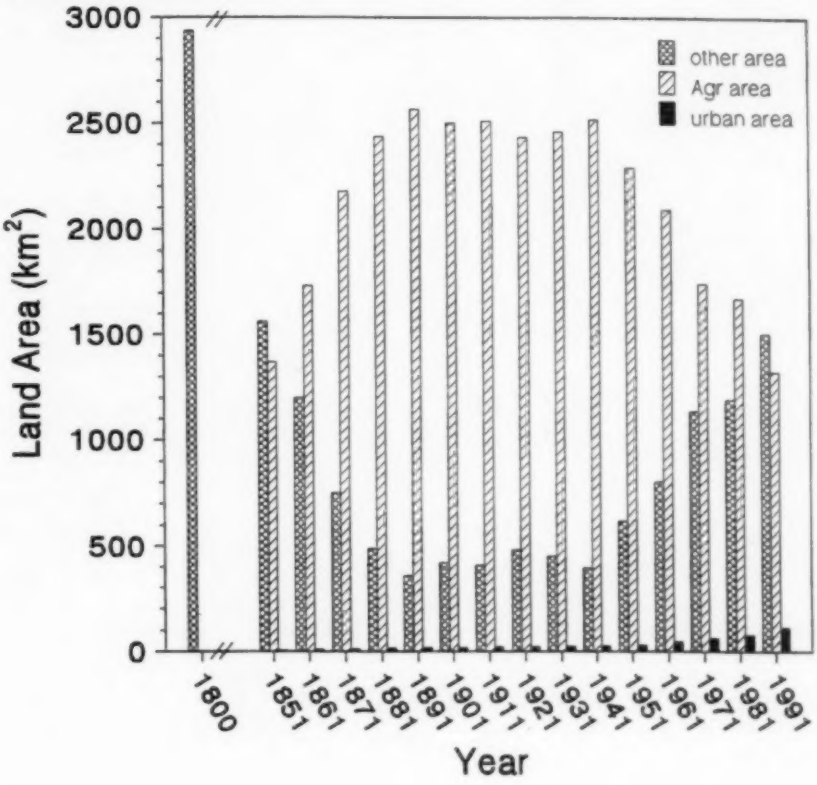
Fig. 3. Land areas in the Lake Simcoe watershed in agriculture, urban (residential, commercial, and industrial), and other (forest, wetlands, scrublands) categories. From Statistics Canada census data summarized by Wilson (1986) and the Lake Simcoe Region Conservation Authority, Newmarket, Ont. (unpublished data).



Urbanization

Urbanization of the Lake Simcoe shoreline (cottages, permanent homes, and resorts) apparently peaked about one-half century ago. Urban growth within the basin and to the south in the vicinity of Toronto and railway access to Lake Simcoe contributed to the use of the lake for recreational purposes as early as 1870 (MacCrimmon and Skobe 1970; Craig 1977). The exclusive resorts catering to the wealthy during the late 1800s and early 1900s were replaced by family resorts and summer cottages after World War II. The number of cottages grew from about 200 in 1920 to about 12 000 by 1970 (Wilson 1986) and has apparently increased only marginally since; however, about one quarter of all lakeshore dwellings are now used year round. Total P loading rate to the lake is now about 5 $t \cdot yr^{-1}$ from shoreline dwellings (Beak Consultants Ltd. 1994). Conceivably, the impact of this source is greater in the Cook's Bay portion of the lake where there is a proportionately higher number of older cottages with malfunctioning sewage treatment systems.

Inputs of nutrients and organic matter from urban sewage to Lake Simcoe likely became significant about the turn of the century, by which time residential, commercial, and industrial developments had become well established on the lakeshore and on rivers draining to the lake. Deteriorating water quality from direct discharge of sewage to surface waters, as well as an increasing concern for the protection of human health, led to the construction of sewage treatment plants (STPs) in 1933 at Aurora, followed by Barrie in 1940, Orillia in 1946, and Uxbridge in 1950. Typically, STP processes evolved over time with the first primitive plants providing only basic primary treatment (removal of some solids). The city of Barrie, for example, implemented full primary treatment in 1952, upgraded to full secondary treatment in 1965, added P removal in 1974–1977, and completed a major expansion in 1988, which included increased capacity and tertiary filtration and effluent polishing with further expansion in 1992 (Gore and Storrie Ltd. 1993).

The present-day plant at Barrie is the largest in the Lake Simcoe watershed and uses an advanced level of treatment technology. Still, the P loading from this plant was estimated at 2–3 $t \cdot yr^{-1}$ for 1990–1992, down from 4–5 $t \cdot yr^{-1}$ for the late 1980s OMEE, unpublished data). Presently, 12 sewage treatment facilities are operating in the Lake Simcoe basin and contribute 5.2 $t \cdot yr^{-1}$ of P to the lake. All sewage treatment effluents are discharged to receiving waters with total P concentrations of 0.1–0.3 $mg \cdot L^{-1}$, which is the current minimum achievable by current technology (Environment Canada 1994; Belmer and Hultman 1988). Maximum allowable P outputs

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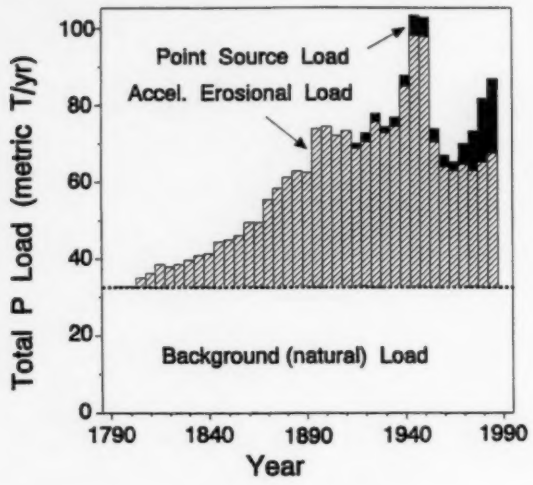
Fig. 4. Historical phosphorus loading to Lake Simcoe as inferred from sediment analyses (after Johnson and Nicholls (1989)).



from these facilities were assigned in 1985 (LSEMS 1985) on the basis of a final P effluent concentration of 0.3 mg·L^{-1} and the hydraulic capacity of each facility at that time.

The significance of urban stormwater runoff is revealed by the changes in specific conductivity and chloride concentration in Lake Simcoe waters, which have increased over the past 20 years (1.34 μmhos·cm^{-1}·yr^{-1} and 0.6 mg Cl·L^{-1}·yr^{-1}, respectively). These changes are due to increasing use of road salt related to expansion of the road network and increased vehicular traffic associated with the expanding human population in the watershed (Nicholls 1995*a*; Fig. 2).

Aquatic ecosystem trends

Phosphorus loading

Phosphorus load to Lake Simcoe sediments pre–1800 was relatively uniform among the four main sedimentation basins of the lake, ranging between 6.26 and 10.65 μg P·cm^{-2}·yr^{-1} (Johnson and Nicholls 1989). After agriculturalization and urbanization of the basin, the distribution of sedimentation changed dramatically, especially in Cook's Bay where sedimentation rate increased by about an order of magnitude and P load increased to 90.94 μg·cm^{-2}·yr^{-1}, apparently in response to conversion of marshes on the lower Holland River to intensive agriculture (Johnson and Nichols 1989). The total area of the sedimentation basins is about 319 km^2 or 44% of the total water area of the lake. The average presettlement P load to the sediments was 8.85 μg·cm^{-1}·yr^{-1} or 28.2 t·yr^{-1} compared with 23.13 μg·cm^{-1}·yr^{-1} or 74.7 t·yr^{-1} for the period 1975–1985. Johnson and Nicholls (1989) determined that the total P load to sediments 10–20 yr before present was comprised of a natural background load of 28.2 t·yr^{-1} (37.8%), an accelerated erosional load of 30.3 t·yr^{-1} (40.6%), and a point-source enrichment of 16.1 t·yr^{-1} (21.6%).

Based on the sediment record and a P retention coefficient of 0.885 (Nicholls 1995*a*), the total presettlement P loading rate to Lake Simcoe waters averaged about 32 t·yr^{-1}, increased steadily to a peak in excess of 100 t·yr^{-1} between 1940 and 1950, declined to about 65 t·yr^{-1} during the early 1960s, and then increased again to present-day (mid–1980s) values of about 90 t·yr^{-1} (Fig. 4). These trends are not entirely consistent with known changes in land use, indicating that the sediment losses hindcast by Wilson (1986) using soil loss estimations were not necessarily correlated with P delivered to the lake. Much of the erosional losses may have resulted in translocation of soil over short distances within a subwatershed boundary, soil that may not have reached Lake Simcoe because of deposition in valley bottomlands. Still, an accelerated soil mass and P sedimentation rate, linked to the period of deforestation and agriculturalization of the Lake Simcoe watershed, was observed from lake sediment cores by Johnson and Nicholls (1988, 1989). Much of the P adsorbed to soil particles possibly sedimented to the lake bottom soon after reaching the lake and may not have been readily available for plant growth.

Point-source P loads have become more important since about 1960 (Fig. 4), coinciding with the dramatic rise in population in the Lake Simcoe basin. With the use of phosphates in laundry detergents in the mid-1940s, the total P content of wastewater in secondary treatment plant effluent averaged 5–7 mg·L^{-1}, about 50% of which was of detergent origin. Federal legislation in 1971 and 1973 limited the P content of laundry detergent to 5% (by weight as P_2O_5). Although a reduction in P loading to Lake Simcoe undoubtedly was achieved by this legislation, the continued human population growth during the past two decades and the associated increased loading from expanded sewage treatment facilities and increased urban stormwater runoff have nullified the gains of phosphate reductions in detergents (Beak Consultants Ltd. 1994). Also, a relatively small fraction of the total P load to Lake Simcoe is from municipal sewage effluents (Fig. 4).

With an annual average contribution of P of about 23.7 t·yr^{-1} (1982–1992) to the lake, the Holland River is the largest single contributor of P to Lake Simcoe (Peat and Walters 1994). Within the Holland River basin, the sources of P include the cultivated Holland Marsh, traditional highland agriculture, municipal sewage treatment plants at Bradford, Schomberg, and until 1984, Aurora and Newmarket. The diversion out of the basin of about 6 t·yr^{-1} of P in sewage effluent from Aurora and Newmarket to the York–Durham trunk line in 1984 appears to have had an affect on the southern end of Cook's Bay, where Secchi disk visibilities averaged 1.7 m in the 5 yr prior to the diversion and increased significantly ($P < 0.05$) by 24% to 2.1 m during the subsequent 10-yr period (Nichols 1995*a*).

Phosphorus concentrations in Lake Simcoe appear to have declined slightly from 1980 to 1992 (Nicholls 1995*b*). Phosphorus concentrations ranged from a high of about 0.023–0.032 mg·L^{-1} in Cook's Bay to a low of 0.012–0.014 mg·L^{-1} in the northeastern sector of the central basin for 11 sampling stations from 1980 to 1992 (Nicholls 1995*a*). Concentrations were lower for the period 1987–1992 compared with 1980–1986 at 10 of the 11 sampling stations, presumably because of diversion and improved treatment of sewage effluents, declining agriculture activity, and other mitigative measures.

Physical limnology

Averaged over all years the mean volume-weighted hypolim-

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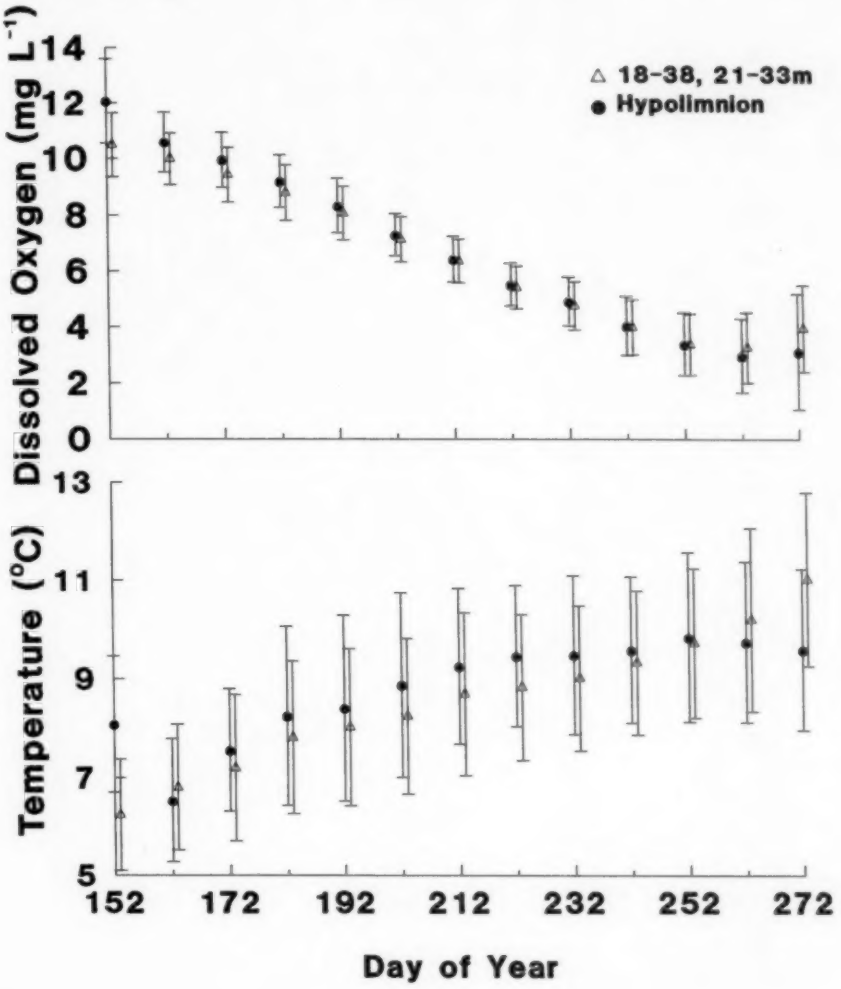
Fig. 5. Seasonal progression of volume-weighted temperature and dissolved oxygen in a constant volume (18–38 m in Kempenfelt Bay and 21–33 m in the central basin) and in the hypolimnion from June 1 (calendar day 152) to September 29 (calendar day 272). Mean values ± 1 SD are indicated for 1975–1993 (n = 19 yr).



netic temperature increased from about 6 ± 1.3°C on June 1 to about 9 ± 1.5°C on August 1 (Fig. 5). Hypolimnetic temperature increased more slowly after August 1 and reached about 10 ± 1.8°C by September 9 (calendar day 252), which was the date of maximum heat content of the hypolimnion (Fig. 5). Volume-weighted hypolimnetic dissolved oxygen concentration declined steadily from a mean of about 12 mg·L^{-1} on June 1 to about 3.0 mg·L^{-1} on September 19 (Fig. 5). The hypolimnion remained isolated from surface effects until about September 19 (calendar day 262), when temperatures begin to decline and oxygen depletion reached a maximum (Fig. 5).

The volume of the hypolimnion at 10-day intervals from June 1 to September 29, was variable from year to year, but there were no upward or downward trends during the years of the study (Fig. 6). The average volume-weighted hypolimnetic temperature within years from August 30 to September 19, 1975–1993, varied markedly from a maximum of about 11.70 ± 1.83°C in 1980 to a minimum of 5.71 ± 0.13°C in 1991. Similarly, mean volume-weighted hypolimnetic dissolved oxygen varied from a maximum of 5.75 ± 0.30 mg·L^{-1} in 1975 to a minimum of 1.35 mg·L^{-1} in 1990. There was an downward trend in both temperature and dissolved oxygen content of the hypolimnion over the period 1975–1995 (Fig. 7). Comparison of deviations of hypolimnetic volume, temperature, and dissolved oxygen, averaged for calendar days 242, 252, and 262, from the long-term means revealed that dissolved oxygen and temperature tended to be lower during the second half of the time series and that volume tended to be about the same (Fig. 8). Multiple regression analysis of the deviations of dissolved oxygen from the long-term trend versus deviations of temperature and volume were not significantly correlated ($P > 0.05$).

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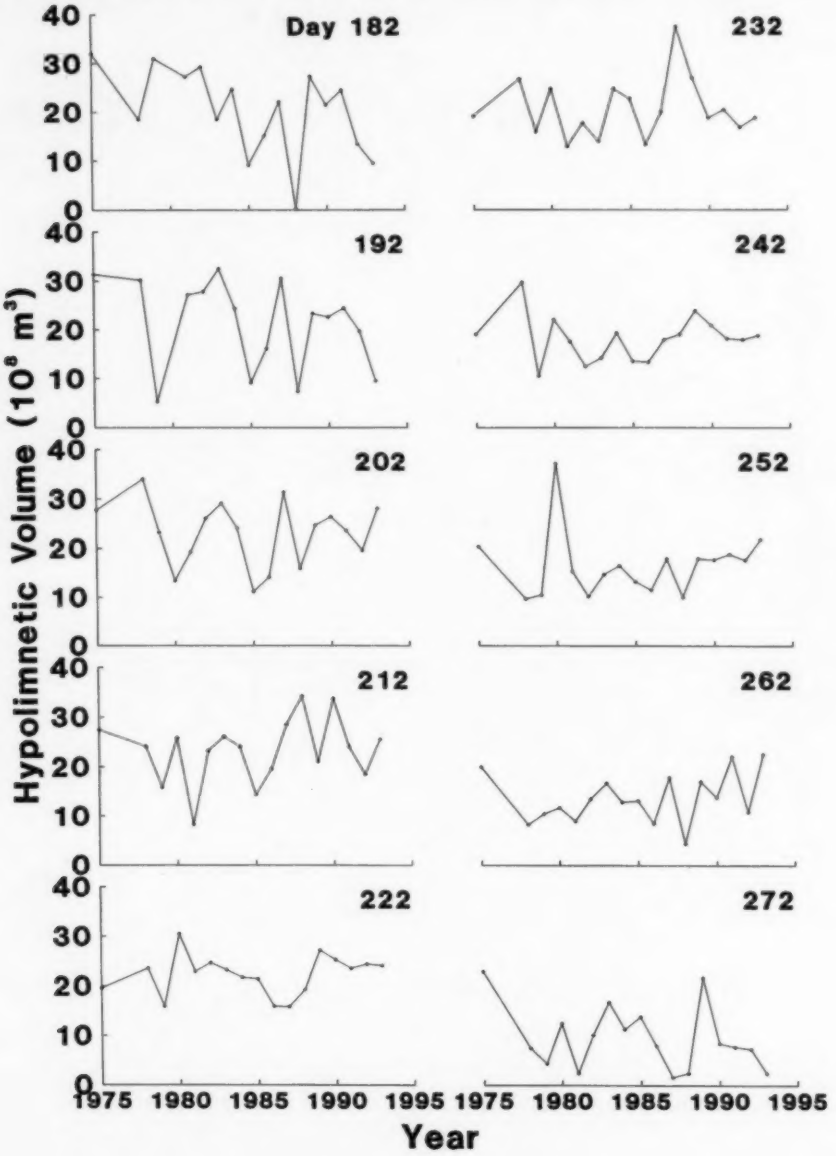
Fig. 6. Interannual variation in hypolimnetic volumes on various dates during the study period. Volumes are indicated from July 1 (calendar day 182) to September 29 (calendar day 272), which corresponds to the period of relatively stable stratification.



Multiple regression analysis of volume-weighted dissolved oxygen concentration (DO_{VW}) versus total hypolimnetic volume (V_{HYP}) and volume-weighted hypolimnetic temperature (T_{VW}) for calendar dates 212–272 over all years, however, revealed that both hypolimnetic volume and temperature were statistically correlated with dissolved oxygen ($F = 34.5$, $P < 0.001$, and $t_{b1} = 7.262$, $P < 0.001$; $t_{b2} = -4.097$, $P < 0.001$, respectively; Fig.9). Hypolimnetic volumes were largest and temperatures were lowest in the spring when dissolved oxygen was highest. Using the empirical relationship: $DO_{VW} = 4.906 + 0.138(V_{HYP}) - 0.315(T_{VW})$ we adjusted the dissolved oxygen content for each year on August 31, September 9, and September 19 to correspond to the mean hypolimnetic volume (1.652×10^9 m^3) and mean temperature (9.85°C) for all years to allow comparisons over years. A significant downward trend in the adjusted hypolimnetic dissolved oxygen concentration on calendar days 242, 252, and 262 of about 2 mg·L^{-1} was evident from 1975 to 1993 (Fig. 10). Oxygen depletion rates in the hypolimnion over days 152–272 also revealed a trend of increasing rates of depletion from 1975 to 1993

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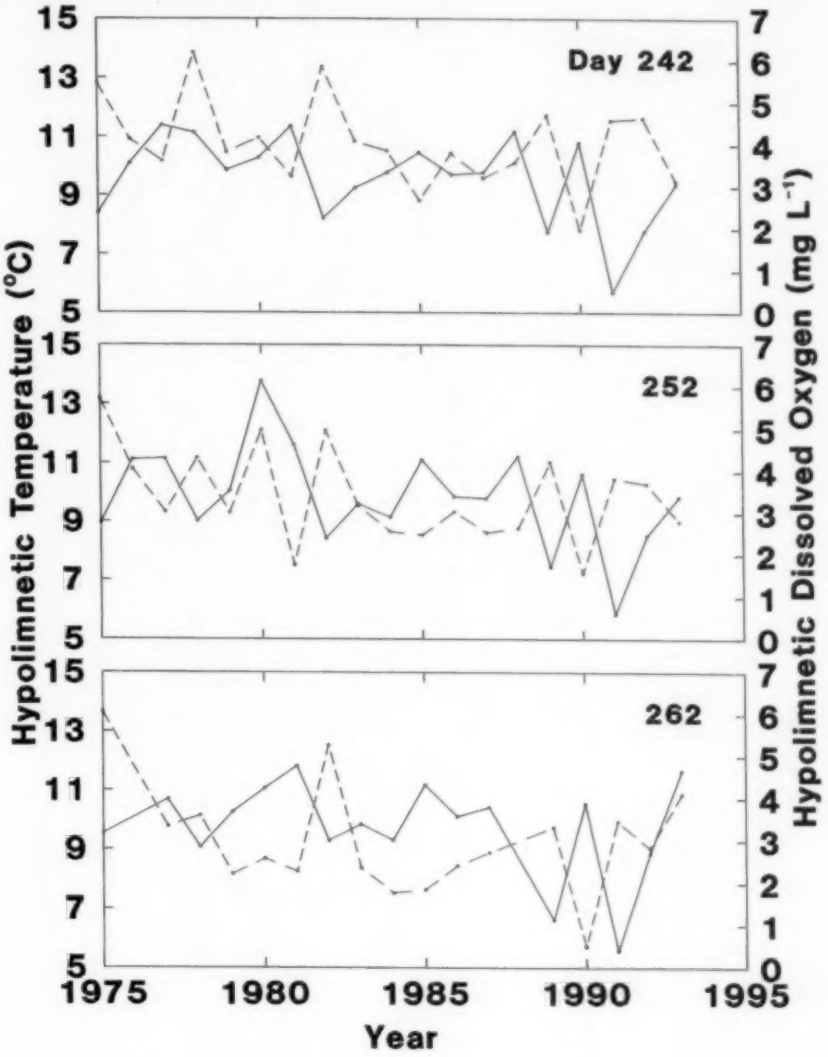
Fig. 7. Interannual variation in hypolimnetic volume-weighted temperature and dissolved oxygen on calendar days 242, 252, and 262, 1975–1993.



(Fig. 11). Oxygen depletion rates within years were not correlated with average hypolimnetic temperature over days 152–272 ($F = 0.692$, $P = 0.417$).

During the study period we observed a downward trend in hypolimnetic temperatures and an increase in oxygen depletion rates. Summer concentrations of dissolved oxygen in the hypolimnion now regularly reach marginal conditions for cold-water fishes, even when calculated on a volume-weighted basis for the whole hypolimnion. During late summer, the mean volume-weighted dissolved oxygen concentration in the hypolimnion often fell to < 3.0 mg·L^{-1} (Fig. 7), which is within the incipient lethal range for salmonid fishes (Davis 1975).

Dissolved oxygen concentrations several metres above the lake bottom in the hypolimnion declined to < 2 mg·L^{-1} during mid-September to early October in most years. During the first 3 weeks of October, in 8 of 11 yr from 1980 to 1990, dissolved oxygen declined to < 1 mg·L^{-1} within the zone 3–11 m from the substrate in the central basin and Kempenfelt Bay. Anoxic conditions were recorded in Kempenfelt Bay in the 36–39 m stratum on October 22, 1980, and in the 32–39 m stratum on October 23, 1985. These observations suggest that P release from anoxic sediments possibly occurred during most years of the study.

Phytoplankton trends

Phytoplankton density has been measured in Lake Simcoe only since 1980. Nicholls (1995*a*) found that phytoplankton

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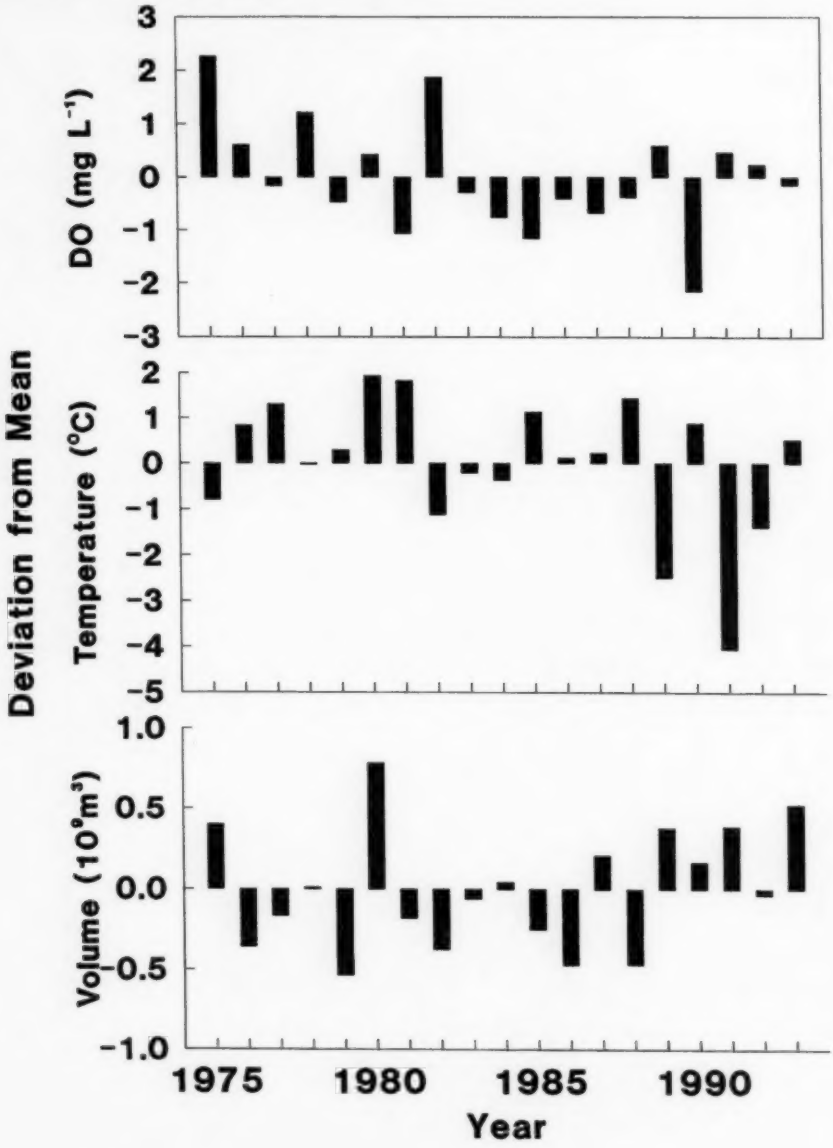
Fig. 8. Deviations from the long-term, mean volume-weighted dissolved oxygen, volume-weighted temperature, and volume of the hypolimnion of Lake Simcoe, on calendar days 242–262, 1975–1993.



densities declined by almost 50% from the early 1980s to the late 1980s and early 1990s in southern Cook's Bay and that the same pattern of decline existed at all 10 Lake Simcoe sampling stations. The decline in phytoplankton density was consistent with a similar decline in P at all but 1 of the 11 lake sampling stations. Nicholls et al. (1985) had earlier reported a strong correlation between P concentration and phytoplankton biomass at various Lake Simcoe sampling stations confirming strong coupling between P and phytoplankton production in Lake Simcoe as is well established elsewhere (Dillon and Rigler 1974*b*). Phytoplankton growth reached an annual maximum during late fall (Hopkins and Webb 1990), which indicated a possible late-summer release of P from the sediments (Nicholls 1995*a*).

Fish community trends

Natural recruitment of lake trout, lake whitefish, and lake herring began precipitous declines about 1960, 1970, and 1980, respectively (Fig. 12). The lake trout stock is now supported entirely by stocking of hatchery-reared yearling lake trout of Lake Simcoe native origin. The lake whitefish stock continues to recruit at a low level, but is also supplemented by hatchery-

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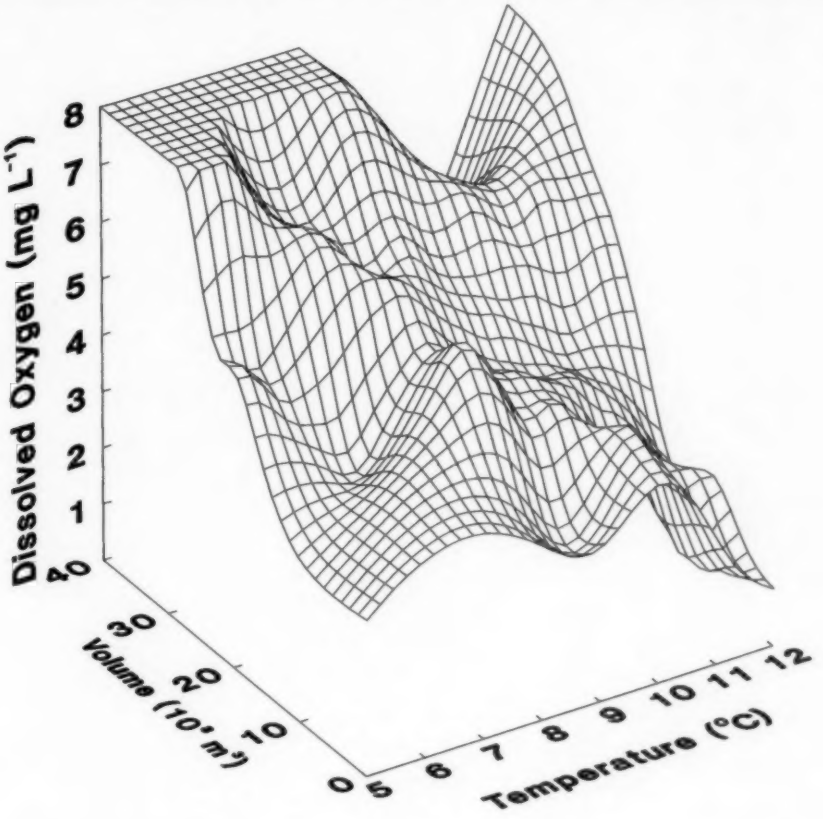
Fig. 9. Three-dimensional surface plot of volume-weighted hypolimnetic dissolved oxygen versus hypolimnetic volume and volume-weighted temperature. Data are restricted to the time when the hypolimnion is usually identifiable (calendar days 212–272).



reared yearlings and fall fingerlings of Lake Simcoe native origin. Lake whitefish of hatchery origin contributed 33% to the winter angling catch and 58% to the spawning run in 1993 (OMNR, Lake Simcoe Fisheries Assessment Unit, Sutton, Ont., unpublished data). Lake herring also appear to be recruiting at a low level and are now at an all-time low population density (Fig. 12). Rainbow smelt, an introduced species in 1961, reached a population peak in 1973 and has subsequently declined to a relatively stable level at about 20–30% of the 1973 level. The decline of rainbow smelt after 1973 is probably attributable to the dramatic increase in the abundance of stocked lake trout after 1975. Rainbow smelt were a prominent prey of lake trout during the late 1970s (DesJardine and Lawrence 1978), 1980s (Burns 1983), and 1990s (Stronks 1994).

Fish distribution and habitat use

Fish catches in gill nets set on the lake bottom during late summer clearly revealed distribution clusters of warm-water and cold-water fishes (Fig. 13). Lake trout, lake whitefish, and lake herring inhabited mean daytime depths > 26 m, while white sucker, yellow perch, and smallmouth bass were found at or above the thermocline at 15–20 m or shallower during September 1982. During September 1983, lake trout, lake whitefish, and lake herring inhabited shallower depths of 22–25 m. The shallower distribution in 1983, and slightly warmer temperatures at capture, appears to be in response to lower dissolved oxygen concentrations in that year (Fig. 14). Lake trout and lake whitefish shifted their distribution to shallower depths in 1983, lake herring shifted only slightly, and rainbow smelt appear to have remained at the same depth during 1982 and 1983. Lake whitefish, lake herring, and rainbow smelt were caught at a mean dissolved oxygen concentration of only 2.0 $mg \cdot L^{-1}$, compared with 3.2 $mg \cdot L^{-1}$ for lake trout. The incipient lethal oxygen level for lake trout is about 3.0 $mg \cdot L^{-1}$ (Gibson and Fry 1954); therefore, they were apparently occupying habitat at dissolved oxygen levels at or immediately above their lethal threshold. Catches in midwater gill nets set at the same time during 1983 indicated that lake whitefish, lake herring, and rainbow smelt tended to move up in the water column more than lake trout. A tendency of lake trout to remain near bottom might explain their move to shallower depths at slightly higher oxygen levels. The other species apparently moved up and down in the water column, presumably to ameliorate the effects of low dissolved oxygen near the lake bottom.

While hypolimnetic dissolved oxygen conditions near bot-

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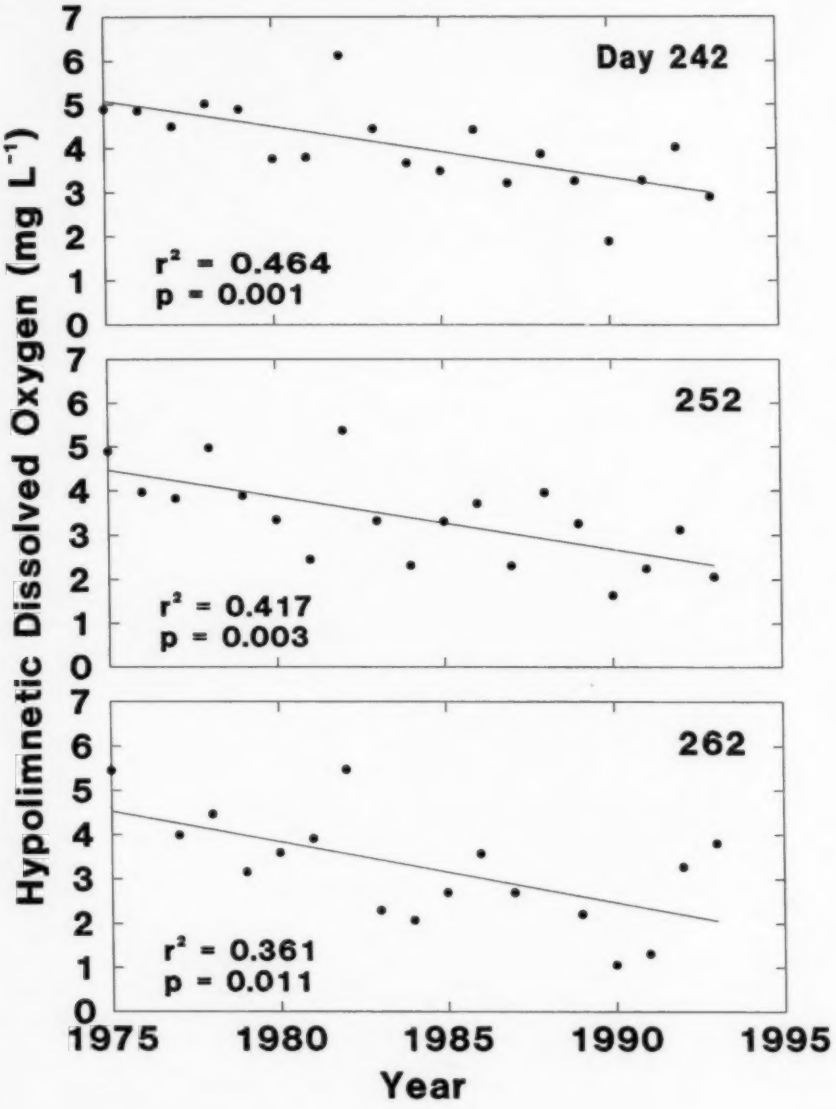
Fig. 10. Volume-weighted hypolimnetic dissolved oxygen concentrations on calendar days 242, 252, and 262. Dissolved oxygen concentrations (DO) were adjusted using a multiple regression of volume-weighted dissolved oxygen versus volume-weighted temperature and hypolimnetic volume for calendar days 212–272 (see Fig. 9). Adjusted volume-weighted DO = observed volume-weighted DO – 0.138(observed hypolimnetic volume – mean hypolimnetic volume) + 0.315(observed volume-weighted temperature – mean volume-weighted temperature).



tom at the depth of the gill nets were lower in 1983 (0.7–2.5 mg·L^{-1}) than in 1982 (3.1–5.4 mg·L^{-1}), lake trout, lake whitefish, lake herring, and rainbow smelt showed remarkable fidelity for the hypolimnetic habitat, even thought they encountered incipient lethal conditions. Dissolved oxygen conditions during September 1982 were among the highest observed during the study, while conditions during September 1983 were intermediate (Fig. 8). Dissolved oxygen conditions during 1981, 1984, 1985, 1987, and 1990 were much more severe than 1983 (Fig. 8). The response and distribution of the cold-water fishes observed during 1983, while near the incipient lethal value for lake trout, were actually relatively moderate compared with conditions in several other years (Fig. 8).

Thermal habitat volume and habitat loss

The average Lake Simcoe thermal habitat volumes for lake trout (8–12°C), lake whitefish and lake herring (7–11°C), and

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Fig. 11. Oxygen depletion rates over the study period for calendar days 172–262 in the hypolimnion and a fixed hypolimnetic volume (18–38 m in Kempenfelt Bay and 21–33 m in the central basin). The upper line indicates the hypolimnetic oxygen depeletion regression (r^2 = 0.410, P = 0.003, n = 19). The lower line indicates the oxygen depletion rate for a constant volume approximating the hypolimnion (r^2 = 0.470, P = 0.001, n = 19). This constant volume is the sum of the 18- to 38-m volume represented by the Kempenfelt Bay station profiles and the 21- to 33-m volume represented by the central basin station profiles.

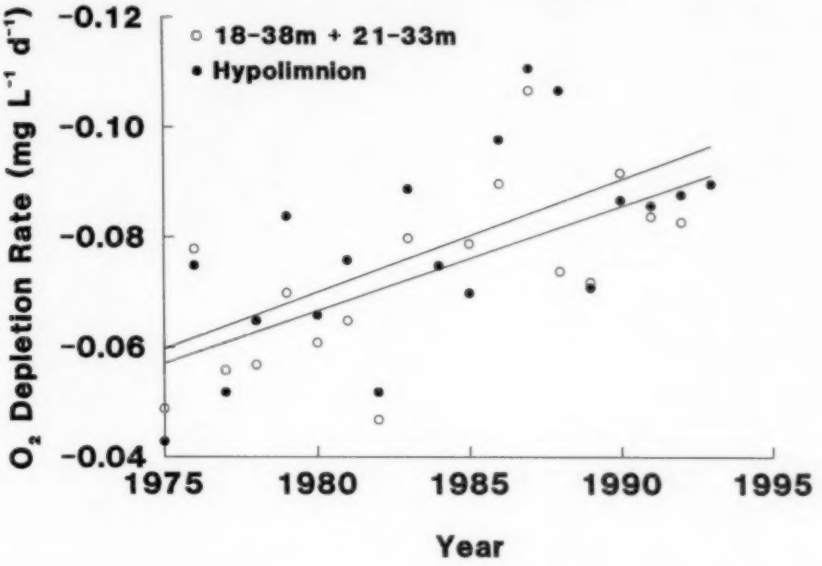

Fig. 12. Angling catches of three native cold-water fish species and the introduced and naturalized rainbow smelt adjusted to a standardized 50-day winter angling season. Solid lines represent total numbers of fish and dotted lines indicate the numbers of wild (unclipped) fish. The break in the lake herring data series represents a change in the length of the angling season, which affected the catch of this species.

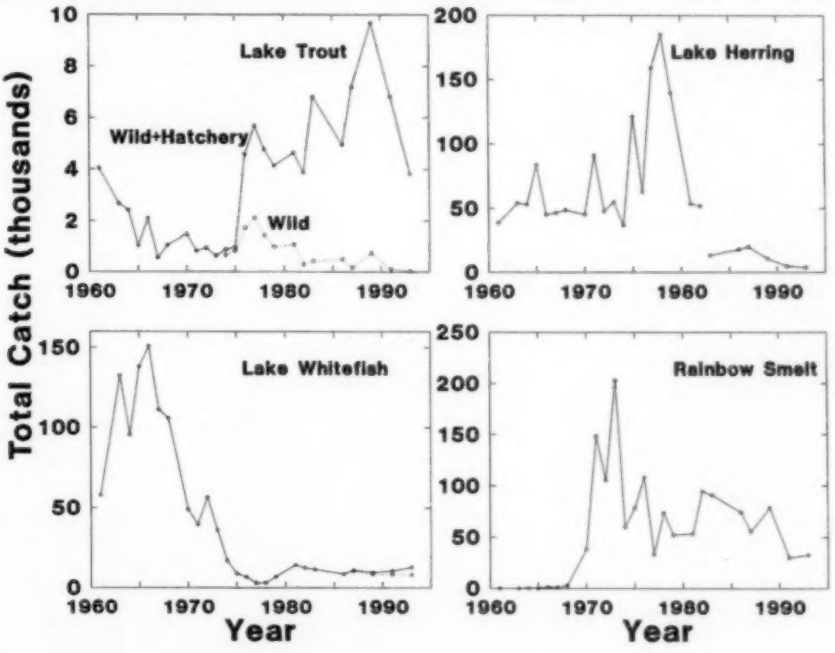

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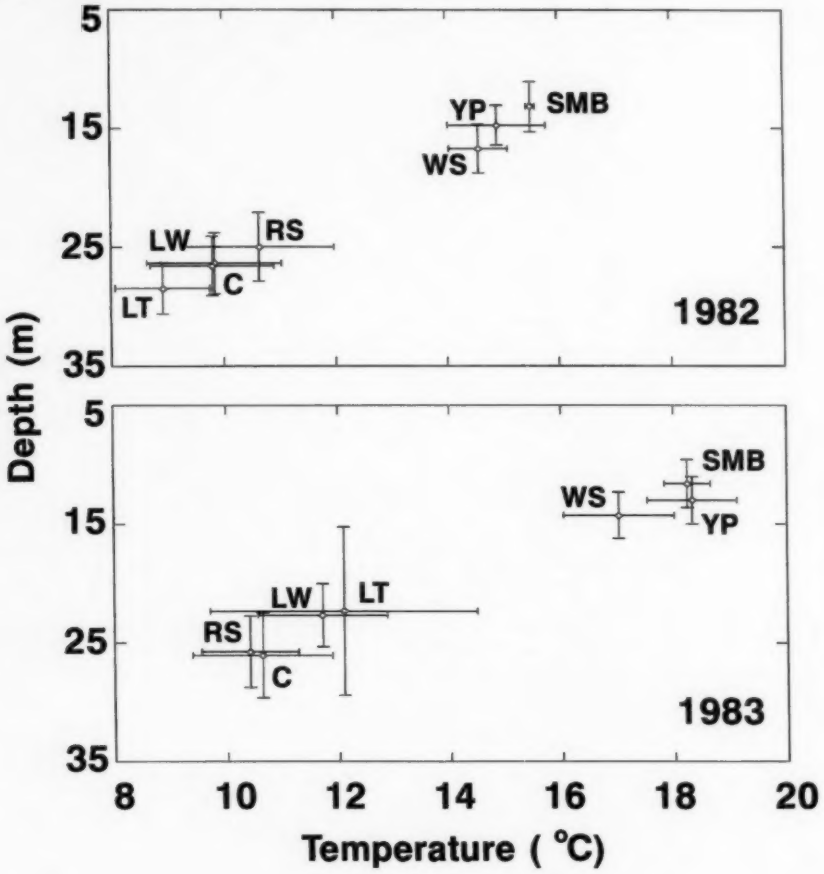
Fig. 13. Mean depth and temperature at capture for seven fish species caught in monofilament nylon gill nets set on bottom during September 1982 and 1983. Gill nets were set at 5-m depth intervals from 5 to 30 m. Depth, temperature, and dissolved oxygen were measured at the net. Depth and temperature calculations were weighted by catch-per-unit-effort at each station. Bars indicate 1 SD for each attribute. Fish species abbreviations are: LT, lake trout; LW, lake whitefish; C, lake herring; RS, rainbow smelt; WS, white sucker; YP, yellow perch; SMB, smallmouth bass.



rainbow smelt (9–13°C) are shown for August 30 to September 19, for the years 1975–1993, in a running series of 4°C temperature intervals corresponding to the observed preferred ranges (Fig. 15). Literature values for these species were approximately 8–12, 10–14, 10–14, and 8–12°C, respectively (Christie and Regier 1988; Evans and Loftus 1987; Wismer and Christie 1987). The thermal habitat volumes were variable but stationary over the time period. There was no optimal habitat (AHV7) available for lake trout, lake whitefish, or lake herring from August 30 to September 19 after 1981, and very small quantities of suboptimal habitat (AHV5) were available in some years only (Fig. 15). Suboptimal habitat also existed in some years for rainbow smelt in the temperature range 9–13°C. Marginal habitat (AHV3) existed for each of the cold-water species within their preferred thermal ranges during all years of the study.

The differences between THV and AHV7, AHV5, and AHV3 expressed as a percentages of THV provided measures of potential habitat lost as a result of oxygen depletion during late summer. For the 7–12°C thermal habitat volume associated with lake trout, lake herring, and lake whitefish, annual losses of AHV7 were essentially constant at 100% after 1982, with 100% loss of AHV5 except for 1975, 1978, 1982, and 1989, when losses varied from 40 to 95%, and losses of AHV3, from 0 (1975, 1982, 1989) to 100% (1990) (Fig. 16). During the summer growth period from June 1 to August 30, only 20–30% of the available cold-water thermal habitat had less than 7 $mg \cdot L^{-1}$ dissolved oxygen when averaged over all years (Fig. 17). Similarly, only 5–15% of the potentially available cold-water habitat had less than 5 $mg \cdot L^{-1}$ dissolved oxygen, and only about 5% had less than 3 $mg \cdot L^{-1}$. By August 30 to September 19 (calendar days 242–262), however, major habitat loss had occurred for the native cold-water species amounting to losses of 60–98% of AHV7, 30–90% of AHV5, and 10–50% of AHV3 (Fig. 18).

During late summer (August 30 to September 19) the ther-

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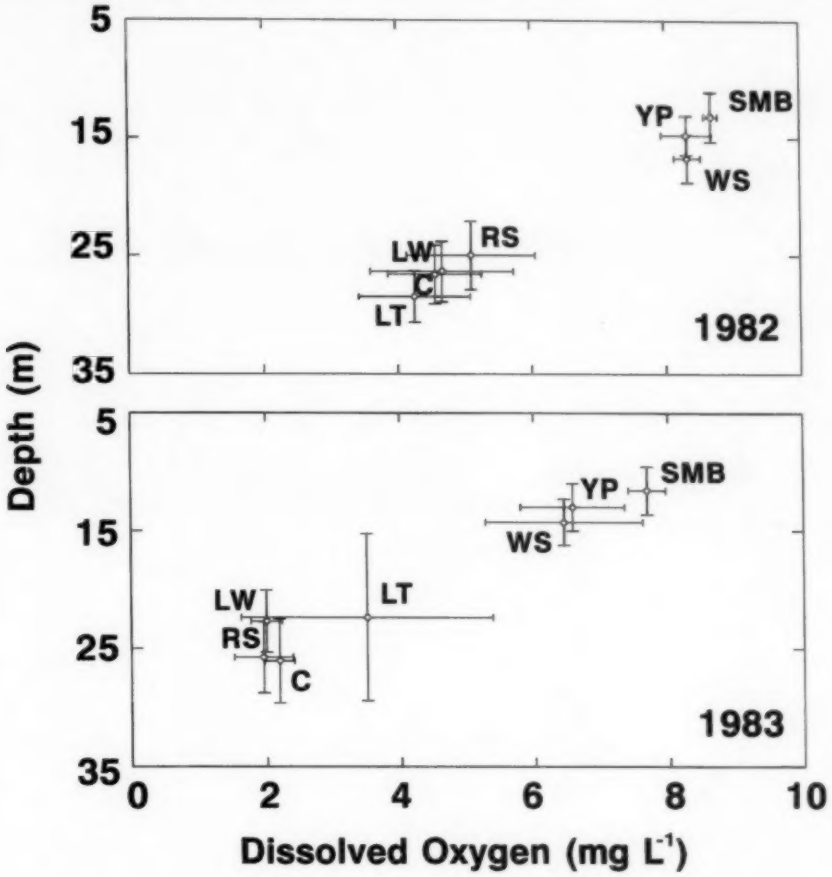
Fig. 14. Mean depth and dissolved oxygen at capture for seven fish species caught in monofilament nylon gill nets set on the lake bottom during September 1992 and 1993. Gill nets were set at 5-m depth intervals from 5 to 30 m. Depth, temperature, and dissolved oxygen were measured at the net. Depth and dissolved oxygen calculations were weighted by catch-per-unit-effort at each station. Bars indicate 1 SD for each attribute. Species abbreviations are as in Fig. 13.



mal regime of Lake Simcoe was most favourable to cool-water fishes, the lake having maximal habitable volumes in the thermal range 14–22°C. The cold-water habitat was limited by the loss of > 80% of the volume < 14°C and > 5 mg·L^{-1} dissolved oxygen, whereas < 5% of the volume > 14°C and > 5 mg·L^{-1} dissolved oxygen was lost to the cool-water species (Fig. 18).

Discussion

Linkages between land use, phosphorus, hypolimnetic dissolved oxygen and fish habitat

Phosphorus loading to Lake Simcoe increased dramatically as a result of land-use changes in the catchment basin over the past 200 yr. Erosion due to deforestation and agriculture accounted for most of the P load during the initial 100 yr (Johnson and Nicholls 1989). Analysis of sediment cores allowed separation of natural background, cultural erosional sources, and enrichment from point sources (Johnson and Nicholls 1989). Point-source P enrichment appeared about 55–80 yr before present and increased dramatically in the most recent sediment layers. Increased point-source loads of P in the sediments corresponded closely to the extensive urbanization that occurred during the past 50 yr. Increased concentrations of chlorides at the Atherley Narrows outlet and in municipal water intakes during the past two decades is a further strong signal of recent population growth and development in the Lake Simcoe basin (Nicholls 1995*a*). Similar increase in chloride was recorded for Lakes Erie and Ontario during the first half of this century (Beeton 1969).

The link between human land-use activities and elevated P inputs to lakes is extensively documented (Ryding and Rast 1989).Water input, hydrology and lake flushing rate, geology and topography of the drainage basin, lake basin morphology, and the presence of upstream lakes have important influences on P loads to water bodies in the absence of human development. Point-source loads from municipal sewage treatment facilities (e.g., Edmondson 1970) and land drainage from nonpoint sources, such as agricultural and urban lands (Dillon and Kirchner 1975), can significantly increase P loads to water bodies.

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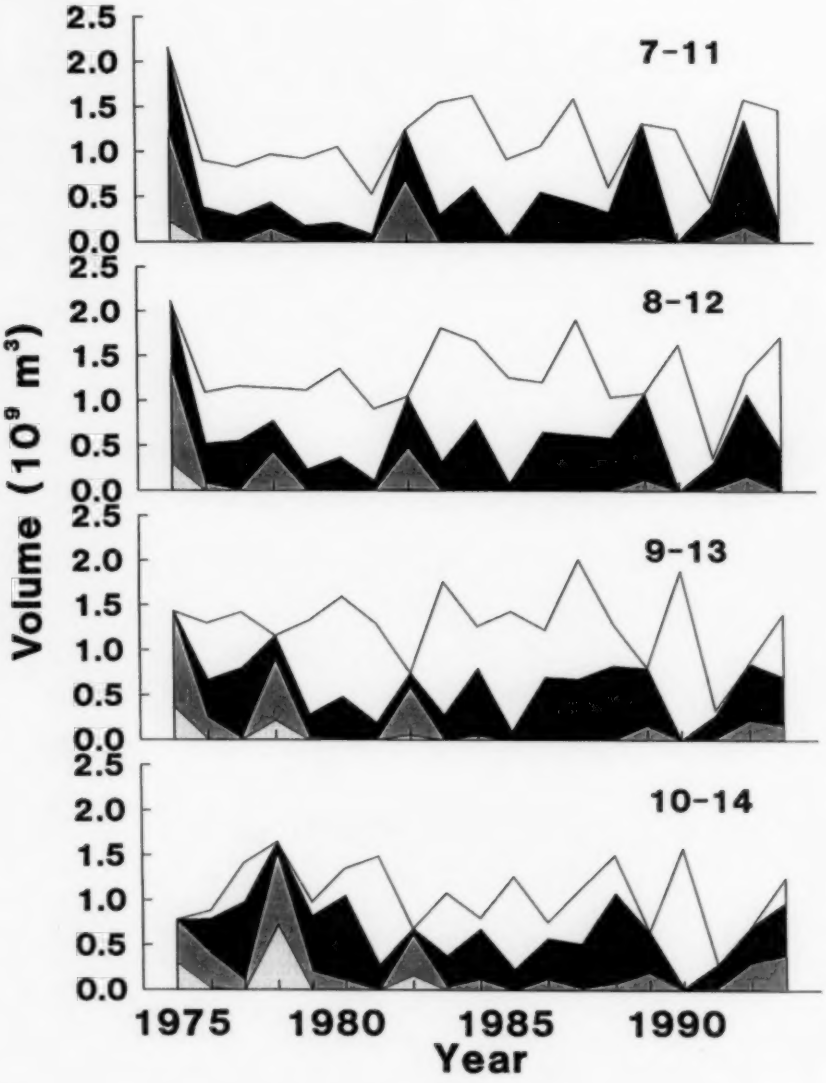
Fig. 15. Interannual variation in thermal habitat volumes (THV) for calendar days 242–262 (August 30 – September 19) during the study period. The thermal habitat ranges (°C) are indicated along the right side of the figure. The amount of actual habitat volume available after constraint by each of three levels of dissolved oxygen criteria, i.e., > 3 mg·L^{-1} (AHV3), > 5 mg·L^{-1} (AHV5), and > 7 mg·L^{-1} (AHV7), is also indicated. The areas indicated for THV (open), AHV3 (solid), AHV5 (dark grey), and AHV7 (light grey) are overlaid and all have their origin at zero.



Changes in the supply of P directly affects P concentrations in lakes (Dillon and Rigler 1974*a*) and the production of phytoplankton, which is often measured as chlorophyll concentration (Dillon and Rigler 1974*b*). Phytoplankton biomass at various locations in Lake Simcoe varied about threefold within years and was strongly correlated ($r = 0.76$) with P concentration at the same locations (Nicholls et al. 1985). Decomposition of the algae in the tropholytic zone of lakes results in depletion of dissolved oxygen in the hypolimnion during the period of summer stratification. The link between chlorophyll and oxygen depletion of the hypolimnion of lakes has been clearly established (Charlton 1980; Vollenweider and Janus 1982). Other researchers have developed P-based models of hypolimnetic dissolved oxygen depletion (Welch and Perkins 1979; Cornett and Rigler 1980, 1987; Cornett 1989; Molot et al. 1992). These models, which in some cases incorporate temperature and lake morphometry variables, have provided field validation of the theory of lake metabolism as based on

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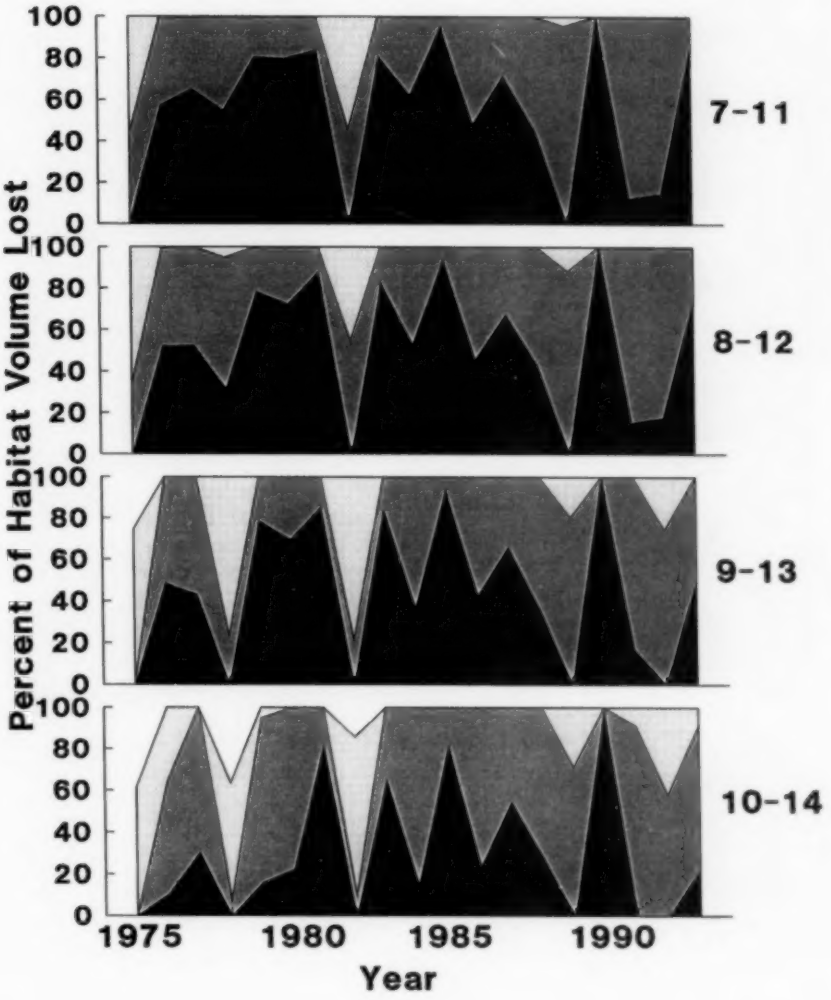
Fig. 16. Amount of thermal habitat volume lost from August 30 to September 19 (mean of calendar days 242–262) because of reduced oxygen availability in the hypolimnion of Lake Simcoe. Habitat loss is calculated as the percent difference in habitat volume from THV for AHV3 (solid), AHV5 (dark grey), and AHV7 (light grey). The areas indicated for AVH3, AHV5, and AHV7 are overlaid, each with their origin at zero.



studies of the individual processes of photosynthesis, respiration (water column and sediment oxygen demand), and vertical transport of dissolved oxygen (Cornett and Rigler 1987).

The evidence presented here documents the dramatic changes in human land-use activity in the Lake Simcoe basin and direct association with increased P loading. The linkage between P loading and increased system primary production is unequivocal as is the linkage between primary production, whole lake metabolism, and depletion of dissolved oxygen in the hypolimnion during summer stratification. Loss of habitat for the cold-water fishes was quantified using the concept of THV and knowledge of the limiting effects of dissolved oxygen on fish activity and respiration. The link between fish production and the quantity and quality of the aquatic habitat is intuitively appealing and supported by published empirical studies (Christie and Regier 1988), but the complexity of the interactions between physical and chemical processes and the requirements of species life stages render elusive definitive conclusions about exact mechanisms of action. For example, recruitment failure of lake whitefish in Lake Simcoe appears to be caused by interaction with the introduced rainbow smelt rather than the direct influence of summer habitat loss (Evans and Waring 1987). Lost access to potential THV, because of low dissolved oxygen, has possibly intensified the spatial interaction between lake whitefish and rainbow smelt, although the negative effect of rainbow smelt on lake whitefish has been observed in many lakes (Evans and Loftus 1987).

Comparison of the P loading trend with the timing of re-

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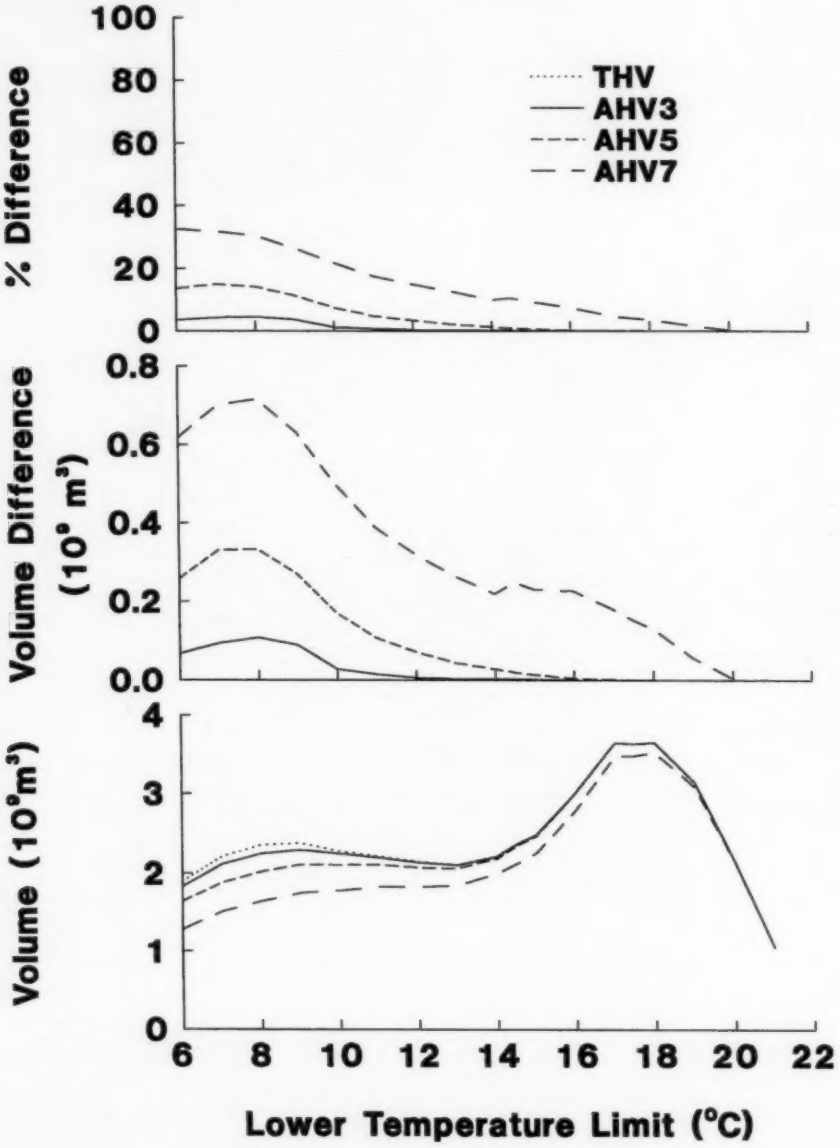
Fig. 17. Average thermal habitat volume and habitat volume lost for calendar days 152–242 (June 1 – August 30) because of reduced oxygen availability. The lower panel indicates the actual volume of habitat within each 4°C temperature interval from 6–10 to 21–25°C. The middle panel indicates the actual mean difference from THV for AHV3 (solid), AHV5 (short dashes), and AHV7 (long dashes). The upper panel indicates the percentage difference in habitat volume (mean of calendar days 152–242) calculated as in Fig. 16. Habitat loss is calculated for all overlapping 4°C temperature intervals from 6 to 21°C at 1°C intervals.



cruitment failure of the cold-water species in Lake Simcoe suggests inconsistencies or time lags between these events. Phosphorus loading peaked about 1890 in the central basin, about 1920 in Kempenfelt Bay, about 1940 in the outlet basin, and about 1945 in the Cook's Bay basin (Johnson and Nicholls 1989, Fig. 5). Recruitment failure of lake trout (1960s), lake whitefish (1970s), and lake herring (1980s) followed the peaks in P loading by several decades, especially in the central basin and Kempenfelt Bay, which provide the main summer refugia for these species. Historical data for hypolimnetic dissolved oxygen prior to 1975 are rare (Evans 1978), so the timing of water quality changes and recruitment failure cannot be readily compared. If loss of hypolimnetic habitat underlies the recruitment failure of lake trout, lake whitefish, and lake herring, an explanation is required for the asynchrony between the temporal trends of P loading and fish recruitment, given that P

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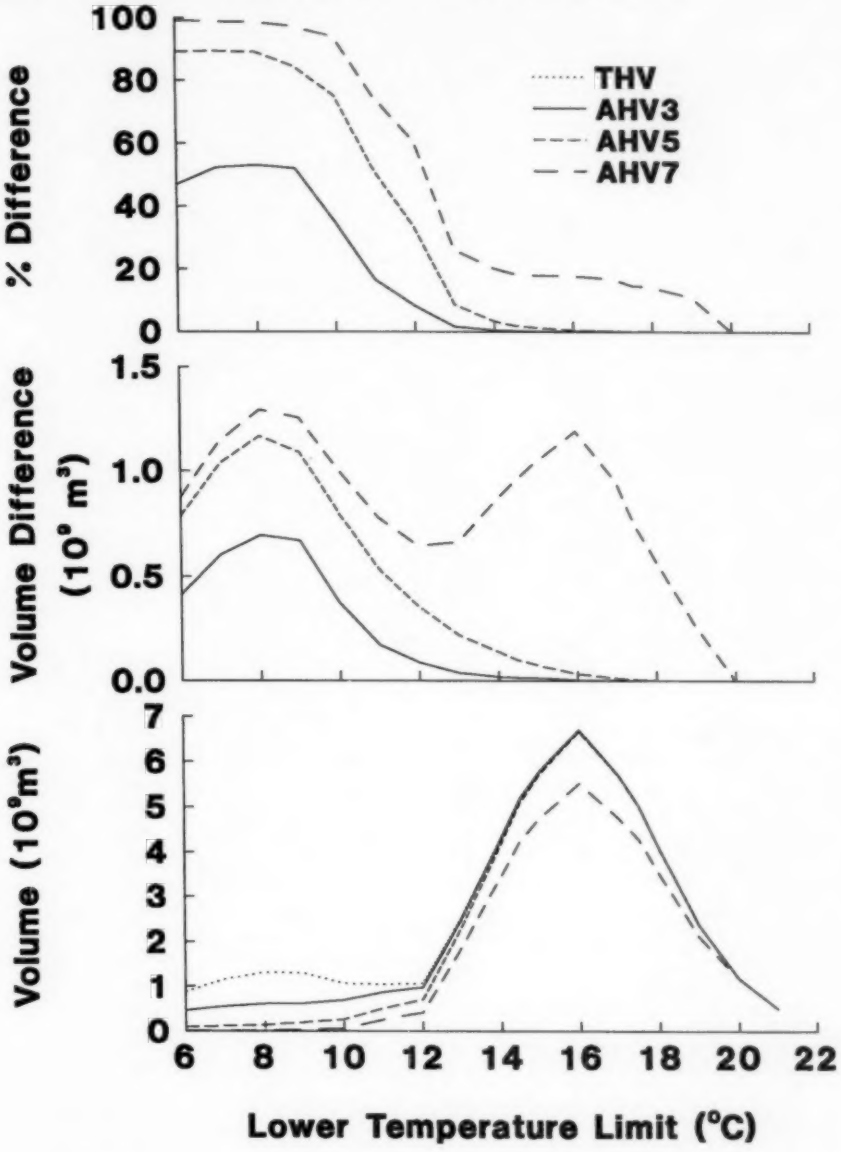
Fig. 18. Average thermal habitat volume and habitat volume lost for calendar days 242–262 (August 30 – September 19) because of reduced oxygen availability. The lower panel indicates the actual volume of habitat within each 4°C temperature interval from 6–10 to 21–25°C. The middle panel indicates the actual mean difference from THV for AHV3 (solid), AHV5 (short dashes), and AHV7 (long dashes). The upper panel indicates the percentage difference in habitat volume (mean of calendar days 242–262) calculated as in Fig. 16. Habitat loss is calculated for all overlapping 4°C temperature intervals from 6 to 21°C at 1°C intervals.



load is tightly coupled to dissolved oxygen depletion rates (e.g., Cornett 1989). The lag between loading and recuitment failure has several possible explanations: (1) the P at peak load was not readily available for algal production; (2) fish behavioural adjustments might have delayed the appearance of the problem as fish utilized suboptimal habitat; or (3) fish recruitment failure might not be directly driven by loss of hypolimnetic habitat.

Phosphorus during peak loads was derived from erosional sources and, therefore, a large fraction of the load was adsorbed to soil particles. These particles probably sedimented rapidly and may not have been readily available to phytoplankton in the euphotic zone. The P loads of the 1960s–1980s were composed of higher fractions from point sources, including the Holland Marsh pump-off water, septic tank drainage, and municipal sewage treatment plant effluents (Fig. 4). Phos-

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phorus from point sources is largely in dissolved form and readily available for algal production (Nicholls and MacCrimmon 1975). Recent analyses revealed that dissolved (filtered reactive) P comprised 68.6 and 80.4% of total P from two Holland Marsh pump-off stations (Peat and Walters 1994). Dissolved P will not sediment to the lake bottom until it is incorporated into algal cells. The P from point sources, therefore, has probably had a greater effect on primary production, hypolimnetic oxygen consumption, and loss of fish habitat than P from erosion of upland areas in the Lake Simcoe catchment basin. Also, as sediment P load increased and oxygen depletion became more severe, internal loading of P from anoxic sediments (Nurnberg 1988, 1991) probably began to be significant, exacerbating the loading of dissolved biologically reactive P from point sources. Occurrence of a major plankton bloom following remixing of the water column in the fall strongly suggests the occurrence of internal loading of P in Lake Simcoe (Nicholls 1995*b*).

Hypolimnetic dissolved oxygen depletion possibly increased during the 1960s, 1970s, and 1980s in response to an increase in biologically available P even though the total P load declined sharply during the 1950s and 1960s (Fig. 4). Extensive dissolved oxygen depletion occurred in Kempenfelt Bay as early as October 1957 (Anderson 1964). Dissolved oxygen was 1.5 $mg \cdot L^{-1}$ at 27.4 m and 1.0 $mg \cdot L^{-1}$ at the bottom (36.6 m) on October 17, 1957, and 1.4 $mg \cdot L^{-1}$ at 27.4 m and 0.0 $mg \cdot L^{-1}$ at the bottom (38.1 m) on October 23, 1957 (D.V. Anderson, OMNR, Maple, Ont., unpublished data). Recycling of biologically available P from the sediments probably occurred at least as early as the mid-1950s. Increased loading of biologically active P from point sources through the 1970s and 1980s was probably responsible for the increasing rate of hypolimnetic oxygen depletion observed from 1975 to 1993 (Fig. 11).

Oxygen depletion and associated loss of cold-water habitat has in fact become more severe during the time period corresponding to recruitment failure of lake trout, lake whitefish, and lake herring; the time lag between these recruitment failures and the peak of total P loading probably can be explained by the greater biological availablity of the P load in more recent times and the attainment of dissolved oxygen thresholds for fish beyond which behavioural and physiological compensation was not possible. In 1975 the end-of-summer hypolimnetic dissolved oxygen was about 4.0 $mg \cdot L^{-1}$, whereas by 1985 it was about 3.0 $mg \cdot L^{-1}$ and by 1990 was 2.5 $mg \cdot L^{-1}$. During the study period mean end-of-summer hypolimnetic dissolved oxygen conditions shifted from sublethal to incipient lethal for lake trout and possibly for lake whitefish and lake herring as well.

The sequential population declines among the fish species is possibly related to differing vulnerability of their life stages to hypolimnetic habitat loss. Juvenile lake trout are dependent on deep benthic habitat (Evans et al. 1991), while young lake whitefish are found on bottom in the vicinity of the thermocline (Reckahn 1970), and young lake herring tend to be suspended near the thermocline (Fry 1937). Our midwater netting also revealed that lake trout were more confined to the lake bottom during late summer than lake whitefish or lake herring. Based on these species differences, lake trout would be expected to be most sensitive to hypolimnetic oxygen depletion, lake whitefish would be intermediate, and lake herring would be most tolerant, which corresponds to the order of recruitment failure observed in Lake Simcoe. While dissolved oxygen depletion is a major stressor on the cold-water species, it is probable that other factors, including interactions with introduced species, have also influenced the success of the native species (Evans and Waring 1987). Thus, the lag between total P load and fish population response can possibly be explained by the greater availablity of the point-source P load, internal P loading, and the associated recent increases in oxygen depletion rates beyond critical thresholds for the cold-water species.

Fish habitat and productive capacity

Sustained yields of lake trout and lake whitefish in large North American lakes have been shown to be correlated with the amount of preferred thermal habitat (Christie and Regier 1988). Optimal growth is known to be strongly correlated with scope for activity (Fry 1971; Neill et al. 1994) and species thermal preferenda (McCauley and Casselman 1981). The amount of thermal habitat expressed as THV, therefore, should be a valid measure of fish productive potential and a useful baseline for evaluation of lost production potential caused by limiting or lethal factors. Measures of THV and AHV (available habitat volume) revealed the relative suitability of the habitat for various thermal guilds of fishes and the amount of potential habitat lost to production at various times of the year. Loss of cold-water fish production could operate through the effects of low dissolved oxygen on scope for activity, as expressed in reduced ability to capture prey and to grow, and through direct mortality, especially of young-of-the-year and juveniles.

Lake trout are cannibalistic and juvenile lake trout are often found on the periphery of the adult distribution, either in littoral areas in Arctic lakes (Johnson 1975, 1976) or the deep hypolimnion in thermally stratified lakes (Evans at al. 1991). As dissolved oxygen in the hypolimnion reaches the avoidance threshold for lake trout at about 4 $mg \cdot L^{-1}$, juvenile trout would be forced to move to shallower strata, which would bring them into closer association with adult lake trout, thereby increasing the risk of predation. Therefore, loss of the deep-water, thermal sanctuary could be critical for juveniles and might in part explain the complete recruitment failure of this species in Lake Simcoe. This explanation, however, does not account for the success of stocked, hatchery-reared, yearling lake trout, which presumably would also require the deep-water summer sanctuary. Strong survival of hatchery-reared, yearling lake trout in Lake Simcoe (Evans and Willox 1991) suggests the possibility of high mortality of wild fish at an earlier life stage (e.g., embryos and (or) young-of-the-year).

In general, fish community production in lakes has been found to increase as primary production increases (Downing et al. 1990). In extreme situations, however, eutrophication can result in lost habitat for cold-water species as has occurred in Lake Simcoe. Fish community production exhibits greater compensatory capacity than individual species production in response to eutrophication. Differential effects on production at the species level can translate to sweeping structural changes at the community level even though total production remains the same (Evans and Waring 1987; Evans et al. 1987). Stocked hatchery lake trout are presently the dominant piscivore in Lake Simcoe and through predation have depressed

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Table 2. Predicted annual total phosphorus loading rates required to achieve volume-weighted end-of-summer dissolved oxygen concentrations of 4, 5, or 6 $mg \cdot L^{-1}$ in the hypolimnion (Snodgrass and Holubeshen 1993) or the 18-m to bottom zone (Nicholls 1995*a*) given two possible present-day loading rates of 80 or 100 $t \cdot yr^{-1}$.

	Nicholls (1995*a*)		Snodgrass and Holubeshen (1993)	
End-of-summer O_2 ($mg \cdot L^{-1}$)	80 $t \cdot yr^{-1}$	100 $t \cdot yr^{-1}$	80 $t \cdot yr^{-1}$	100 $t \cdot yr^{-1}$
4	75	94	68	89
5	63	78	52	72
6	51	64	35	55

the abundance of rainbow smelt and possibly lake herring (Fig. 12). In the absense of stocked lake trout a very different scenario would unfold in which the fish community would be dominated by small planktivores, similar to the period of great abundances of alewife in the Great Lakes during the 1960s (Wells and McLain 1972; Christie 1972). Oligotrophication and restoration of natural recruitment of lake trout would not only eliminate the ongoing and substantial costs of rearing and stocking, but would also result in a self-regulating and self-sustaining fish community dominated by native species.

Phosphorus loading and dissolved oxygen modelling

Recent attempts to apply both deterministic (Snodgrass and Holubeshen 1993) and empirical (Nicholls 1995*a*) modelling to quantify the dissolved oxygen - total P loading rate relationship have been made. The Snodgrass–Holubeshen approach yielded a prediction of hypolimnetic dissolved oxygen as a function of water column total P, dissolved organic carbon, and sediment oxygen demand. As a mechanistic model, it involved multiple Monte Carlo simulations whereby distributions rather than single values were specified for input parameters. The modelled output was re-evaluated, with new values randomly selected from the specified probability distributions of the input variables. Model calibration was achieved by adjustments of the sediment oxygen demand values and P settling velocities (Snodgrass and Holubeshen 1993).

Nicholls (1995*a*) developed empirical relationships between P load and P concentration, and P concentration and chlorophyll for Lake Simcoe. Nicholls then used the regression model of Vollenweider and Janus (1982) to evaluate predicted and measured tropholytic zone oxygen depletion rates in Lake Simcoe as a function of tropholytic zone chlorophyll concentration and the ratio of trophogenic zone to tropholytic zone volumes. From the predicted oxygen depletion rates normalized to 4°C, end-of-summer dissolved oxygen concentrations were then determined assuming a volume-weighted dissolved oxygen concentration in mid-June of 11 $mg \cdot L^{-1}$ and a volume-weighted average temperature during the mid-June to mid-September period in the 18 m to bottom zone of 8.4°C (14-yr average). For predictive purposes, it was then possible to relate end-of-summer dissolved oxygen concentrations to chlorophyll, P concentrations, and P loading rates through the empirical relationships among these variables.

Both approaches predicted remarkably similar end-of-summer dissolved oxygen concentrations over a range of P loadings of 50–150 $t \cdot yr^{-1}$. Both models hindcast a presettlement, end-of-summer hypolimnetic dissolved oxygen concentration of about 8 $mg \cdot L^{-1}$. Although hindcasting required extrapolation beyond the data range of these models to a presettlement P loading rate of 32 $t \cdot yr^{-1}$, the prediction seemed reasonable (Nicholls 1995*a*). Present-day concentrations of 2–3 $mg \cdot L^{-1}$, therefore, represent a significant deterioration over the past two centuries in the habitat for cold-water species. Both approaches also generated similar predicted changes in total P loading rates that are required to achieve target, end-of-summer oxygen concentrations (Table 2). The models indicated that a 50% reduction in P loading would be required to restore an end-of-summer, hypolimnetic dissolved oxygen concentration of 6 $mg \cdot L^{-1}$, which would be a vast improvement for cold-water species and provide a suitable, if not optimal habitat.

Phosphorus loading controls

Late summer depletion of dissolved oxygen in the hypolimnion has been recognized as the most serious water quality issue in Lake Simcoe (Veal and Clark 1970; Ralston et al. 1975; LSEMS 1985, 1995). A statistically significant increasing trend in dissolved oxygen depletion rates has been measured during the past 19 years (Fig. 11; Nicholls 1995*a*). The trend of increasing dissolved oxygen depletion is apparently out of phase with the stable or declining trend in total P in the euphotic zone from May to October. This is probably partly explained by the changing composition of the P load and partly by the response time dynamics of the lake to changes in P loading. Response time of dissolved oxygen depletion to reduction in P load depends on the P loading rate, P sedimentation rate, flushing rate of the lake, and the residual oxygen demand accumulated in the bottom sediments. Response time estimates for dissolved oxygen depletion are not available, but would probably be in the order of years to decades (Nicholls 1995*a*).

The primary goal of the Lake Simcoe Environmental Management Strategy is improvement of the deep-water habitat for cold-water fishes, the latter being recognized as a useful indicator of ecosystem health in oligotrophic lakes (Edwards et al. 1990). Increased P loading over the baseline natural loads of approximately 32 $t \cdot yr^{-1}$ (Fig. 4) of pre-European settlement times have contributed to excessive production of organic matter and its subsequent decomposition in the hypolimnion of the lake. A decrease in the dissolved oxygen deficit would be expected, if improved management of agricultural and urban development activities could reduce the loading of P to the lake.

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During the past decade, some significant reductions in total P loading to the lake have been achieved. Approximately 6 $t \cdot yr^{-1}$ were diverted out of the Lake Simcoe basin when treated sewage effluents from the towns of Aurora and Newmarket were diverted to Lake Ontario via the York–Durham trunk sewage line in 1994. As well, because of improvements to the Barrie sewage treatment plant, annual loadings to Kempenfelt Bay during the 1990s were about 50% lower than during the early 1980s (LSEMS 1985, 1995). In addition, there have been major efforts to decrease P input from agricultural sources, including fencing to control cattle access to streams, improved treatment of dairy wastewaters, and implementation of conservation tillage practices intended to control erosion of cultivated farm lands. Although there is some evidence for improved water clarity in southern Cook's Bay after 1984 (Nicholls 1995*b*) and decline in total P concentrations in lake water, hypolimnetic dissolved oxygen depletion rates have continued to increase.

Although constituting only about 3% of the drainage basin area, urban lands contribute 30% of the total P loading to Lake Simcoe. Only about 5% of this originates from sewage treatment facilities, the remainder is from urban runoff (LSEMS 1995). Human population and urban area in the basin has doubled in the past 20 years. Gains made in controlling P loading to the lake from sewage treatment facilities and from agricultural activities have apparently been lost because of increased export of P from urban runoff.

If significant reductions in total P loading to Lake Simcoe are to be achieved, some innovative approaches to managing urban runoff will be required. Further reductions are needed at farms not yet practicing conservation tillage, where control of cattle access to streams and manure management practices are still inadequate, and at pump-off locations in the Holland Marsh where excessive P concentrations still exist. Control of urban runoff is more problematical because of the potentially large volumes of water requiring containment and treatment. This issue is an important priority under Phase II of the LSEMS programme (LSEMS 1995). Apparently, the recently applied levels of pollution control have stabilized P loading, but the large reductions in P loading that are required to restore cold-water fish habitat have barely begun and are clearly the major challenges over the next decade and beyond.

Phase II of the Lake Simcoe Environmental Management Strategy has identified six key action areas for environmental management: agriculture practices; urban land-use; recreational activities; monitoring and scientific studies; public awareness, education, and community action; and conservation of natural heritage features (LSEMS 1995). Twenty-eight issues and associated actions have been identified within these key areas. The proposed actions are focused primarily on further control of P loading to the lake, improved quantification of P dynamics, and monitoring of fish community responses. The accelerating point-source P load associated with urban growth is a major environmental management concern. Urban stormwater runoff and sewage treatment effluent are the major sources of P from urban development. The do-nothing option would allow P loads to rise to 107 and 114 $t \cdot yr^{-1}$ by the years 2001 and 2011, respectively (LSEMS 1995). These loadings would result in severe conditions for cold-water fishes. Even without further increases in P loading, continuation of the present trend in hypolimnetic dissolved oxygen depletion to 2005 would result in estimated mean volume-weighted hypolimnetic dissolved oxygen concentrations of about 1–2 $mg \cdot L^{-1}$ from late August to mid-September (Fig. 10). These conditions would be extremely stressful, if not directly lethal to the cold-water fishes. Application of all currently available remedial measures to control P inputs was estimated to have the potential to reduce loading by about 35–65 $t \cdot yr^{-1}$ (LSEMS 1995). This level of control should provide for significant improvement in cold-water fish habitat (Table 2). Restoration and ecological sustainability of the native cold-water fish community of Lake Simcoe is dependent upon achieving and exceeding these P reduction targets.

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Diadromy and the assembly and restoration of riverine fish communities: a downstream view

R.M. McDowall

Abstract: Analysis of predominantly diadromous freshwater fish faunas suggests that migration through the sea is important in establishing and structuring riverine fish communities by dispersion, especially at low elevations and close to the sea coast. This same process is considered profoundly important, also, for facilitating restoration of freshwater fish faunas after perturbation. This is demonstrated for a diversity of New Zealand situations, including maintenance of fish faunas in streams on small islands that may frequently become dry, recent volcanism in the central North Island, and Pleistocene glaciation on the west coast of the South Island. Similarly, diadromy has a probable role in the restoration of fish faunas following retreat of glaciers in Alaska from Pleistocene to modern times. The postglacial biogeography of freshwater fishes along boreal Atlantic and Pacific coasts of North America is reinterpreted in the context of faunas containing a high proportion of diadromous species. Although migratory fish in the Great Lakes are not strictly diadromous, their patterns of movement closely resemble diadromy, and the principles governing the restoration of migratory fish communities in the Great Lakes may be similar to those that apply to restoration along oceanic coastlines where the importance of diadromy seems obvious.

Résumé : L' analyse des faunes piscicoles majoritairement diadromes porte à croire que la migration en mer joue un rôle important dans l'établissement et la structuration par dispersion des communautés piscicoles riveraines, notamment aux faibles altitudes et à proximité des côtes marines. Il semble que ce processus s'avère extrèmement important au moment du rétablissement des faunes piscicoles d'eau douce après une perturbation. Cela est démontré pour diverses situations en Nouvelle-Zélande, notamment le maintien de faunes piscicoles dans des cours d'eau de petites îles qui s'assèchent souvent ou celles ayant trait à une activité volcanique récente dans le centre de l'île du Nord et à la glaciation pléistocène sur la côte ouest de l'île du Sud. De façon similaire, la diadromie a probablement contribué au rétablissement des faunes piscicoles après le retrait des glaciers en Alaska, entre le Pléistocène et les temps modernes. La biogéographie post-glaciaire des poissons dulcicoles le long des côtes boréales de l'Atlantique et du Pacifique de l'Amérique du Nord est réinterprétée dans le contexte de faunes comportant une proportion élevée d'espèces diadromes. Les poissons des Grands Lacs effectuant des migrations ne sont pas strictement diadromes, mais le régime de leurs déplacements présente une allure fortement diadrome et les principes régissant le rétablissement de communautés piscicoles migratoires dans les Grands Lacs pourrait bien être semblable à ceux qui régissent le rétablissement le long des côtes océaniques, où l'importance de la diadromie apparaît clairement.
[Traduit par la Rédaction]

Introduction

Diadromous fishes are truly migratory species (sensu Northcote 1984) whose distinctive characteristics (Myers 1949; McDowall 1988, 1992) include that (*i*) they migrate between fresh waters and the sea; (*ii*) the migration involves all or a majority of the population or cohort; (*iii*) the movement is usually obligatory; and (*iv*) migration takes place at fixed seasons or life stages.

The key criterion is the first of these. Among fish that move to and from the sea, there is a continuum from those that are strictly diadromous to those that are facultative marine wanderers, as a result of which there is in some species difficulty in allocating them to one or other category of lifestyle; nevertheless, for most fish, there is little difficulty in allocation, and where there is difficulty it is due as much to inadequate knowledge of the species as it is to difficulties in classification. Although diadromy is very much a minority phenomenon in the world of fishes (perhaps about 230 species; McDowall 1988), it can be locally important, as is the case in New Zealand and some other lands.

The fish faunas of the rivers and streams of New Zealand are distinctive in their high proportion of diadromous fishes, with 17 of about 30 recognised species (57%) falling into this category (McDowall 1990). This high proportion is unusual. There are some sparse faunas on sometimes highly isolated islands in which the small but entire fauna is diadromous, as in Hawaii (Kinzie 1991), but it is true also of Newfoundland (Hammar 1987). However, impoverished though the New Zealand fauna may be (McDowall 1990), no other fish fauna with the same or a larger number of species has such a high proportion of diadromous fish. The fact that so many species migrate to and from the sea has highly significant implications for (*i*) the patterns of distribution and dispersal in the fauna, (*ii*) the way fish communities are assembled in streams, and (*iii*) the way stream communities recover from serious perturbation. Although the proportion of species that is diadromous in river systems along the oceanic margins of boreal North America is lower than in New Zealand, there is nevertheless a substantial number of diadromous species there, and issues

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relating to the assembly and structuring of the fish communities that apply in New Zealand apply also in North America.

Similar issues apply to the fish faunas of the Great Lakes. Although migratory species in these lakes and their tributaries are not strictly diadromous, since no migrations between the sea and fresh water are involved, quite a few fish in the Great Lakes are landlocked stocks of normally diadromous species, and they undergo patterns of movement in the lake systems that are otherwise comparable. Examples are sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseudoharengus*), and the various Pacific salmons and rainbow trout (*Oncorhynchus* spp.), which undertake upriver migrations from the lakes in much the same way as their ancestors did in Atlantic and Pacific coast seas and rivers. Other non-diadromous Great Lakes fishes migrate between the lakes and their tributaries. There, too, there are similar implications for the assembly and structuring of the fish faunas in the lake tributaries.

The question of open or closed ecological communities

There has for some years been lively debate about the way ecological communities are assembled, and in particular, whether they are controlled by stochastic or deterministic processes (Grossman et al. 1985; Reice 1994). A parallel debate has addressed the biotic or abiotic control of community organization (Power et al. 1988; Dunson and Travis 1991) or whether they are equilibrial or not (Sale 1991). These apparent dichotomies, however, need to be seen as the extremes of a continuum. Moreover, ultimately, the inevitable conclusion has to be that no single model can be developed that describes the way all, or even most, communities are structured (Townsend 1989, and references therein; Dunson and Travis 1991). This has become a recurring call in the ecological literature, e.g., "we should probably abandon attempts to develop a simple unifying theory to explain community patterns" (Wiens 1994), although this should not inhibit the search for generalities of diverse sorts that assist in understanding and classifying ecological community processes. Nor is a community always controlled by one or other mechanism. May (1986) pointed to the prospect that some populations may be undergoing density-dependent regulation at relatively high densities, possibly also at low densities, but are controlled by density-independent fluctuations over much of their observed ranges of densities. Similarly, there is a view that communities may be regulated by deterministic (biotic) factors when environmental conditions are stable for a long period but by stochastic processes during and following short periods of major habitat disturbance, as during floods. May (1986) found much of this argument "sterile semantics" and suggested that "there are no grand generalizations, 'no inverse square laws' of ecology, no naive dichotomies into density-dependent and density-independent populations, or into equilibrium and nonequilibrium communities."

I would like, here, to point to another apparent "naive dichotomy." The different ways that communities are assembled and structured must depend to some extent on whether they are open or closed, though this distinction does not seem hitherto to have attracted much attention (but see Sale 1991), particularly in the study of stream fish communities. Although in the recent past much emphasis has been placed on the role of proximate ecological processes and effects in controlling community structure, there is now a move towards growing emphasis on the role of historical processes. There are, for instance, extensive discussions of the way freshwater fish communities are assembled and structured. These discussions tend to focus on the historical processes that govern the assemblage of species that develops in a stream or lake (Gorman 1991); Bayley and Li (1992), for instance, write explicitly that in riverine fish communities the "formation of species assemblages depends on zoogeographical limits derived in evolutionary time scales." Again, we are faced with the need to integrate both proximate and historical influences (Ricklefs and Schluter 1993). The fact that fish communities are seen by some workers in primarily historical terms (Gorman 1991; Bayley and Li 1992) implies that the species present have reached that habitat through long-term, geohistorical processes such as stream capture and, further, that community dynamics, relative species abundances, and niche characteristics are controlled by processes that occur more or less isolated within the community and its physical setting. They can be either stochastic processes strongly influenced by physical disturbances, like floods, droughts, etc., and (or) deterministic processes depending on interactions within the biological community there (Gorman and Karr 1978; Grossman et al. 1985; Strange et al. 1992). Such communities could be described appropriately as closed. (Note that I do not mean closed and open in the thermodynamics sense of Johnson (1994), but rather in terms of whether the species "list" in a community is relatively fixed and changes only by occasional chance immigrations or extinctions, i.e., is closed, or is continually being invaded from beyond its boundaries, i.e., is open.)

Sale (1988, 1991) has examined the assembly and structuring of the fish communities on small patches of tropical coral reefs and has found that, in some instances, the species present on one reef vary greatly over time and just as greatly between reefs. Eggs and larvae of coral reef fishes are almost exclusively pelagic (Sale 1988), and Sale attributes the composition of the fauna of a reef at any time to what species happen to be in the proximity of "openings" in the community at the time that "space" becomes available. Thus, it could be argued that the assembly of such a community is controlled largely by real- or ecological-time events and by circumstances that lie partly outside the community itself. Such a community could be described as open. A closed stream or lake community and an open coral reef community perhaps represent extremes in what is undoubtedly another continuum, but I think the distinction is worth drawing and bearing in mind when considering the way communities are assembled and structured.

This, I believe, is potentially another of May's (1986) naive dichotomies, of which he was well aware; to quote May, further: "ecology is a science of contingent generalizations where future trends ... depend [both] on past history and on the environmental and biological setting." Understanding the relative roles of these two temporal scales (past history and contemporary setting) profoundly influences the way that community structuring is viewed (Ricklefs and Schluter 1993).

My reason for drawing attention to this distinction is because I think that the occurrence of diadromy in freshwater stream fish communities shifts such communities from being towards the closed extreme of this continuum to being well

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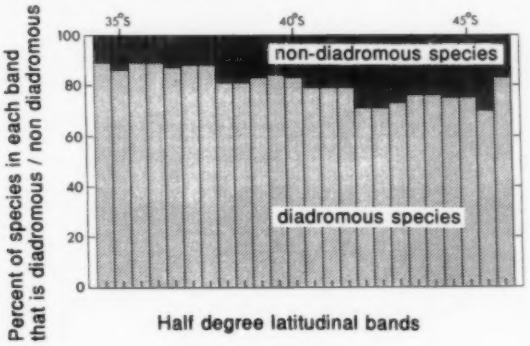
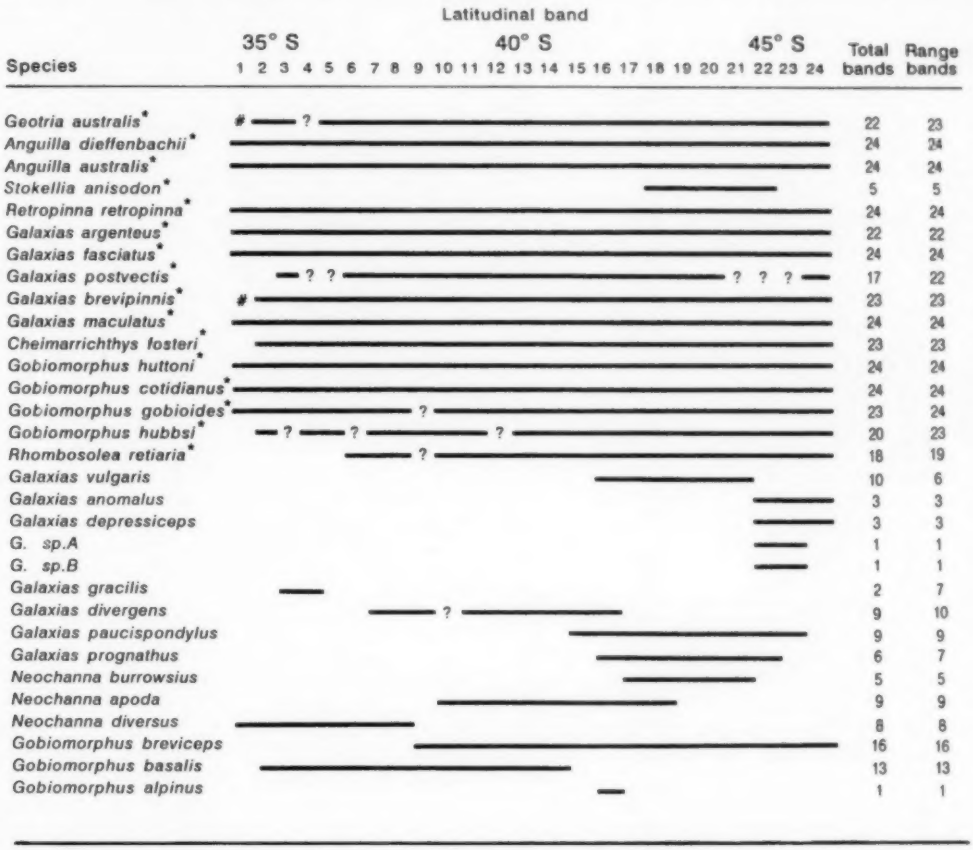
Fig. 1. Percentage of the New Zealand freshwater fish fauna that is diadromous at various latitudes.



towards the open end. Generalizations made by Gorman (1991) and Bayley and Li (1992) about communities being formed in evolutionary time become distinctly dubious when diadromy is a common phenomenon in stream faunas, as it is in New Zealand and along boreal North American coastlines. Because diadromous species invade a community from outside, it is no longer restricted just to the species (individuals and progeny) already present there, and the species mix may vary depending on what migratory species are available to occupy any space present. The processes of invasion and occupation of niches have some parallels with Sale's (1988, 1991) coral reef faunas. (This is especially true for catadromous and amphidromous fishes in which the freshwater invasion is undertaken by small juveniles that can be expected to suffer heavy mortalities in early freshwater life.) Particularly in New Zealand, where so many of the species are diadromous, the stream fish communities have to be understood in terms of

Fig. 2. Number of 0.5°-wide latitudinal bands in which diadromous and non-diadromous New Zealand freshwater fish species are found.


Latitudinal band
35° S
40° S
45° S
Species
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
Total bands
Range bands
Geotria australis* 22 23
Anguilla dieffenbachii* 24 24
Anguilla australis* 24 24
Stokellia anisodon* 5 5
Retropinna retropinna* 24 24
Galaxias argenteus* 22 22
Galaxias fasciatus* 24 24
Galaxias postvectis* 17 22
Galaxias brevipinnis* 23 23
Galaxias maculatus* 24 24
Cheimarrichthys fosteri* 23 23
Gobiomorphus huttoni* 24 24
Gobiomorphus cotidianus* 24 24
Gobiomorphus gobioides* 23 24
Gobiomorphus hubbsi* 20 23
Rhombosolea retiaria* 18 19
Galaxias vulgaris 10 6
Galaxias anomalus 3 3
Galaxias depressiceps 3 3
G. sp.A 1 1
G. sp.B 1 1
Galaxias gracilis 2 7
Galaxias divergens 9 10
Galaxias paucispondylus 9 9
Galaxias prognathus 6 7
Neochanna burrowsius 5 5
Neochanna apoda 9 9
Neochanna diversus 8 8
Gobiomorphus breviceps 16 16
Gobiomorphus basalis 13 13
Gobiomorphus alpinus 1 1

*, diadromous species

#, species likely to occur on bases of distribution beyond New Zealand

?, species likely to occur on bases of distribution elsewhere in New Zealand

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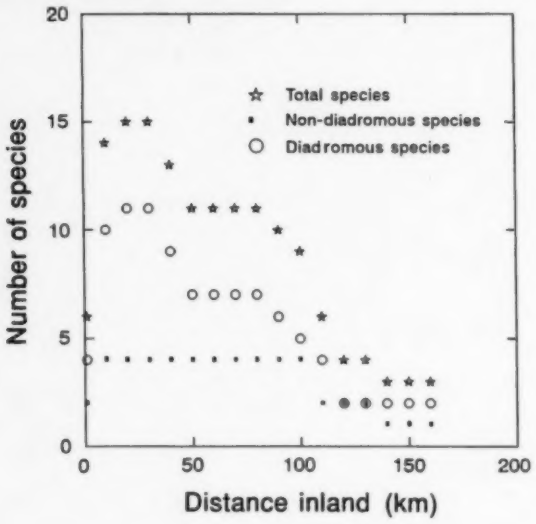
Fig. 3. Changes in species diversity in diadromous and non-diadromous fish species with distance inland in the Grey River, New Zealand.



their being assembled and structured partly under the influence of invasive processes that lie completely outside the ecological communities that form. This is another continuum that could easily be in danger of becoming one of May's "naive dichotomies."

The role of diadromy in the New Zealand freshwater fish fauna

When an analysis is undertaken of the composition and distributions of New Zealand freshwater fish communities, the predominance of diadromy in the fauna becomes even more evident. If the country is divided into 0.5° latitudinal bands and the number of diadromous and non-diadromous species present in each band is computed, it is found that in any band, always more than 70% and usually more than 75% of the species recorded is diadromous, even though at the national level the figure is 57% of the fauna (Fig. 1).

The reason for this is simple: most diadromous species are present in virtually all bands, from north to south (14 of 16 extant diadromous species occur across 22 or more of 24 bands; Fig. 2), and clearly the fact that they have regular marine life stages lasting several months means that they are able to disperse widely in the New Zealand region. Distribution patterns are determined in real or ecological time by biological processes such as dispersal through the sea. By contrast, non-diadromous species are typically present in much fewer latitudinal bands (13 of 15 non-diadromous species occur in 10 or fewer of the 24 bands), and their distributions are more determined in historical or geological time by geomorphological processes; dispersion away from the area where they evolved is often difficult, and slow, so that the geographical ranges of non-diadromous species are much more limited in extent. Furthermore, the most species-rich communities occur at low elevations and close to the sea, and consist almost entirely of diadromous species.

This interpretation of dispersion patterns is supported by comparisons of the genetic structuring of the species. Allibone and Wallis (1993) showed that, whereas several diadromous species in the New Zealand fauna showed virtually no genetic structuring between locations (signifying gene flow between populations), non-diadromous species exhibited substantial genetic structuring (implying a lack of gene flow).

Analysis of distribution patterns of species within river systems shows a general gradation from high species richness at low elevations and near the sea (and a predominance there of diadromous species) to reduced species richness at higher elevations or distances inland. This is occasioned primarily by the loss of diadromous species, a decline that has nothing to do with habitat suitability. The number of non-diadromous species does not vary much with elevation or distance inland, e.g., in the Grey River (Fig. 3), but there is an increasing proportion of non-diadromous species (the number of which is always low (less than five) owing to the loss of diadromous species inland). The downstream-upstream decrease in species richness is different from an apparently similar gradation that is predicted by the rivers continuum concept (Vannote et al. 1980), which is related to increasingly diverse habitats and trophic niches in the downstream reaches of river systems. With diadromous fish, the change in richness has much more to do with access and upstream migration. It is a natural outcome of the fact that diadromous species vary in their upstream migratory instincts and abilities (McDowall 1993). Some species tend to be largely lowland or coastal plains species, and there is a continuum involving others that penetrate further inland and that may occur widely at all elevations within their ranges. There is little evidence for any of the diadromous species occupying only inland locations; the species that do penetrate long distances inland are, in nearly all instances, widespread also at low elevations and near the sea coast and are usually more abundant there than further inland.

In the main, New Zealand riverine fish ecosystems need to be seen as being distinctly open, and assembled by waves of diadromous fish penetrating upstream and occupying those appropriate habitats that they are behaviourally able to reach and that are available in an ecological or invasive sense.

Application to boreal North America

The sorts of distributional trends discussed for the New Zealand freshwater fish fauna seem likely to apply to patterns of distribution and invasion in North America, particularly the boreal, freshwater fish fauna. To the extent that the faunas of boreal coasts of North America and the tributaries of the Great Lakes are made up of migratory species originating in the sea or the lakes, they too will be assembled by waves of migrants penetrating upstream to occupy fluvial habitats. It is well known that some Pacific salmon species such as chinook salmon (*Oncorhynchus tshawytscha*) may penetrate inland much greater distances than pink (*O. gorbuscha*) or chum salmon (*O. keta*), that osmerid smelts (f. Osmeridae) tend to be rather poor immigrants, that amongst the shads some such as American shad (*Alosa sapidissima*) may penetrate considerable distances (up to 600 km; thus much less than some salmon), but that alewife may go only 40 km upstream, and

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blueback herring (*A. aestivalis*) reach little beyond the tidal limits (reviewed in McDowall 1988). This sort of variation in penetration is likely to produce gradients in species richness similar to those observed in New Zealand (R.M. McDowall, unpublished data), though I know of no comparative analysis.

In the context of this paper, the same sorts of patterns of varying penetrations and gradients in species richness of migratory species are likely be true of migratory fish species in tributaries of the Great Lakes. Thus, these riverine fish communities, whether in New Zealand or North America, bear some similarity to the scenario described by Sale (1988), in which there is a pool of immigrants seasonally or periodically available to invade space that appears in the community. The great difference, of course, is that coral reef fish communities have a vastly greater pool of species from which to derive their faunas, so that the species composition of the communities may vary greatly from place to place and time to time. Diadromous freshwater fish communities undergo the same sorts of invasion pressures, but they involve a much more impoverished fauna and they receive seasonally regular invasions by the same species. They need to be seen as substantially open communities, because of the role of diadromous migrations in controlling their assembly in real or ecological time.

The role of diadromy in restoring fish communities after perturbation

While it might be claimed that all habitats (whether marine, terrestrial, or freshwater) are ephemeral, it can also be argued that freshwater habitats are amongst the most ephemeral of all. While New Zealand has many hundreds of lakes, most of them are quite young (< 10 000 years old; Lowe and Green 1987). It is probable that none of them is more than about 20 000 years old, and that some of them have been profoundly perturbed by extensive volcanism as little as 1800 years ago (McDowall, in press). Whether or not there has been time for the evolution of a rich and varied ichthyofauna, it has not happened, and lake fish faunas in New Zealand are extremely impoverished (McDowall 1990). Many lakes in other countries, however, are of course much older, though those in boreal North America are of similar general ages to those of New Zealand, their formation being influenced by the late Pleistocene glaciations (Pielou 1991). Rivers, by nature of their very elongate, threadlike form, are easily subject to major perturbations by rockslides, impoundments, headwater stream capture, dewatering, relocation or redirection of channels by seismic activity, upstream pollution, defaunation by volcanic lahars, and so on. Perturbations that affect terrestrial ecosystems, such as the climatic and physical effects of glaciation and desertification, also often affect river ecosystems just as much. The biogeographical histories of freshwater fish faunas are often largely and intimately involved in the impacts of these river-changing perturbations. Riverine fish faunas often respond slowly and incompletely to these changes, and where recent change has been traumatic for fish species, impoverished faunas are a common outcome.

However, again, when we turn to diadromous fishes, we encounter a different situation. I would like now to point to some more explicit case histories or situations where it seems, at least implicitly, that the way freshwater fish faunas have recovered after perturbation has been significantly affected by diadromous migrations. Fairly obviously, just as diadromy leads to widespread ranges and low genetic structuring in fish species, it also provides a mechanism whereby fish can naturally and rapidly be restored to streams in which there has been an extirpation event, once such streams again become habitable. Even where there is quite precise homing to natal streams, as is well documented in many salmonids, the error rate is high enough to permit repopulation of defaunated streams (Thorpe 1994). In the simplest possible terms, we are dealing with the role of diadromy in dispersion, with the fact that diadromous fishes are continually probing upstream from the sea into those river systems that lie within their marine geographical ranges, and that this provides a rapid and effective mechanism for restoration of fish populations following perturbation. Their role in dispersion and restoration can be seen in several scenarios, from broad patterns of distribution to fine detail of colonization and community development.

The disjunct occurrences of New Zealand freshwater fishes

The only freshwater fish species common to two or more of Australia, New Zealand, and Patagonian South America are diadromous ones (Fig. 4); this seems unlikely to be coincidental. Their broad range is a likely result of dispersal and thus related to diadromous habits (McDowall 1990).

Non-diadromous New Zealand freshwater fishes seem often to ignore Cook Strait, which is only about 19 km wide at its narrowest, and separates the North from the South Island of New Zealand. Perhaps no more than 10 000 – 20 000 years ago it was dry land (Fleming 1979; Lewis and Carter 1994). Several non-diadromous species present in the vicinity of the strait are found on both sides of it and probably occupied the whole area when the sea level was lower (Fig. 5). However, in spite of this, no non-diadromous fish is found on any of the small nearshore islands that are common around New Zealand's coastline, all of which were probably connected to the main islands during the same lowered Pleistocene sea levels. Probably this is because freshwater habitats on these small islands are ephemeral. The islands became disconnected from the mainland as sea levels rose in postglacial times and they lost any freshwater fishes present when their small streams became temporarily dewatered. Only diadromous species are now present on these islands presumably because they have been able to recolonize island streams once, and for as long as, they again became habitable by fish.

Central North Island New Zealand volcanism

The central North Island of New Zealand has, over a period of 25 000 years, been affected by huge and repeated volcanic eruptions (at least 26 times), including the largest recorded eruption in the past 5000 years. Volcanic activity continues today. The area constitutes the most active and productive rhyolitic volcano known (Wilson 1993; Wilson and Houghton 1993). Only about 1800 years ago, there was a vast eruption. Tephra (volcanic ash) was discharged from the magma reservoir, in what is now Lake Taupo (Fig. 6), to feed the most violent pyroclastic flow yet recorded. The material ejected from the vent rose 40–50 km into the air; the collapse of the

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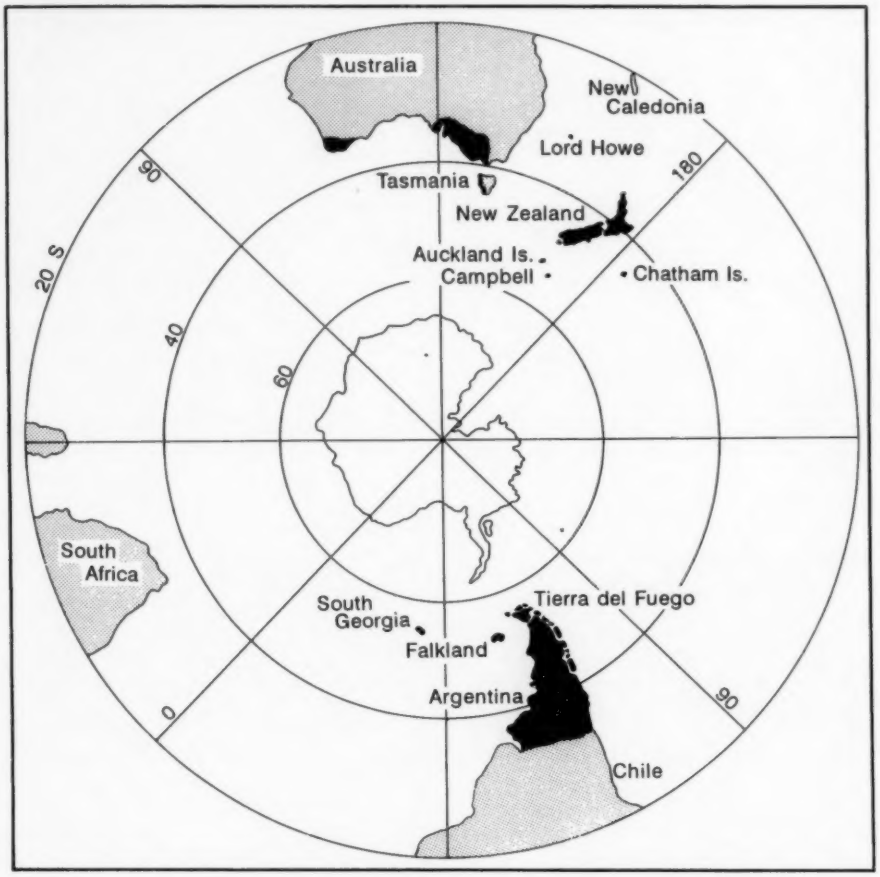
Fig. 4. Distribution of pouched lamprey (*Geotria australis*), representative of diadromous species in Australia, New Zealand, Patagonian South America, and associated islands.



eruption column produce a pyroclastic flow that surged radially at speeds variously estimated at 600–1000 km·h^{-1}, and traveled as far as 80 km from the vent. The momentum of the discharge was such that it covered the tops of mountains 1500 m above the adjacent ground level within that 80 km radius, completely smothering the peaks of mountain ranges in the vicinity. Less dense materials in the eruption column were dispersed eastwards by prevailing winds to cover the eastern North Island with pumice to a depth of at least 10 cm as far as the coast, more than 200 km away (Wilson 1993). Some estimates suggest deposition of ash at sea to a depth of 15 cm as far as 800 km offshore, or 1000 km from the eruption site (Carter 1994). An area of 20 000 km^2, mostly east of the eruption site, is thought to have been devastated (quite apart from impacts in seas beyond the eastern coastline). The total discharge from this last eruption has been estimated at 105 km^3; by comparison, the eruption of Mount St. Helens has been estimated as 1 km^3 and of Mount Pinatubo 20–30 km^3 (Carter 1994). Material discharged from the last Taupo eruption caused colour change in northern hemisphere skies at the time (Wilson and Houghton 1993) and this is said to have been chronicled by contemporary Roman and Chinese writers.

Impacts of Taupo volcanism on freshwater ecosystems can only have been catastrophic. Immense ash-laden floods would have flowed down rivers, possibly for decades. Where ash deposition reached the coast (to the east and northeast), nothing living would have survived. In long rivers that originate within the zone of ash deposition and drain into countryside that was little or not affected, the river main stems would have been defaunated by ash-laden floods from the central zone. However, smaller tributaries that drained topography outside the ash zone may have retained fish faunas. Because the last eruption was so recent (ca. 1800 years ago), its impacts should still be discernible in distributions of stream fishes. Non-diadromous species should be absent from areas covered by ash, and perhaps more widely. However, where these fish persisted in tributary streams that lay outside the ash zone, repopulation of upper reaches would have taken place from downstream refuges, and some of the rivers especially to the north, south, and west, would once more have non-diadromous fish faunas.

Because of their ability to disperse around New Zealand coasts through the sea, diadromous species would have been able to reinvade all of the rivers once the effects of ash-laden

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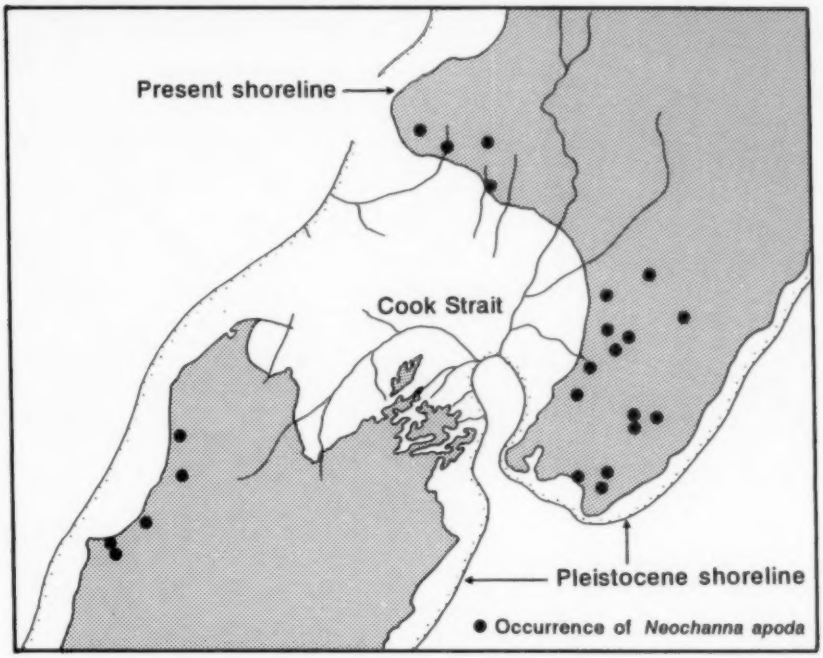
Fig. 5. Distribution of brown mudfish (*Neochanna apoda*) in the vicinity of Cook Strait, New Zealand.



floods abated. Therefore, these rivers should be populated by diadromous species such as eels, just as they are elsewhere in New Zealand. An inspection of the distributions of freshwater fish largely supports this hypothetical scenario. Rivers that now drain east, entirely or mostly through the ash zone, are largely devoid of non-diadromous fish. Occasional populations of non-diadromous fish are present around the margins of the ash zone to the northeast (Figs. 7A–7C). But, as predicted, they are widespread in rivers that drain north, south, and west from the central North Island, these being rivers whose lower tributaries, being beyond the zone of ash deposition, provided refuges for fish.

Diadromous longfinned eels (*Anguilla dieffenbachii*) are widespread there (Fig. 8), and other diadromous species such as shortfinned eels (*A. australis*); common smelt (*Retropinna retropinna*); koaro (*Galaxias brevipinnis*); inanga (*G. maculatus*); torrentfish (*Cheimarrichthys fosteri*); and common, (*Gobiomorphus cotidianus*), redfinned (*G. huttoni*), and bluegilled bullies (*G. hubbsi*) also occur in these catchments, though less widely than longfinned eels, primarily because they customarily penetrate inland less distance than longfinned eels.

Clearly, the occurrence of diadromy allowed species such as longfinned eels to recolonize the badly affected eastern catchments of the central North Island once aquatic habitats became inhabitable. Recolonization by fish, which are in all instances generalized invertebrate predators (McDowall 1990), would have had to follow recolonization of these rivers by benthic invertebrates, but this would have been accomplished more easily since so many invertebrates have flighted terrestrial adult life stages.

Distributional data on these rivers comparable with those available for fish are not available for most benthic invertebrates that do not have flighted or terrestrial life stages. However, the macrocrustacean crayfish, *Paranephrops planifrons* (Crustacea: Parastacidae) has a pattern of distribution comparable with the non-diadromous fish species, being largely absent from eastern catchments (except in Lake Waikaremoana, where prehistoric Polynesian Maori translocation is suspected) (Fig. 7D).

The role of diadromy in facilitating the restoration of catchments defaunated by the Taupo eruptions seems clear.

West Coast South Island glaciation

In common with other lands (Pielou 1991), New Zealand experienced extensive Pleistocene to Quaternary glaciations. The Quaternary was a period when there was vigorous mountain building, volcanism, construction of gravel plains and, throughout, alternation of glacial periods with interglacials. It was a time when much of the contemporary New Zealand landscape was constructed, and was the baseline for the development of still existing patterns of biotic distributions. During the last glacial advance of the Otiran glaciation, ca. 14 000 years BP, ice extended below the present sea level in Fiordland, and entirely covered most of South Westland (Fleming 1979) (Fig. 9); the area is still glaciated, with active glaciers descending to elevations little above sea level (ca. 200 m). The more heavily glaciated southern river catchments of the west coast and Fiordland must have been largely defaunated by the advance of ice. Main (1989) has postulated that this is reflected in the fact that non-diadromous fish species, though widespread in northern West Coast catchments (such as the Buller, Grey, and Hokitika rivers and sometimes present as far south

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Fig. 6. Distribution of ignimbrite flows and ash deposits resulting from eruptions about 186 A.D. from Lake Taupo, central North Island, New Zealand.

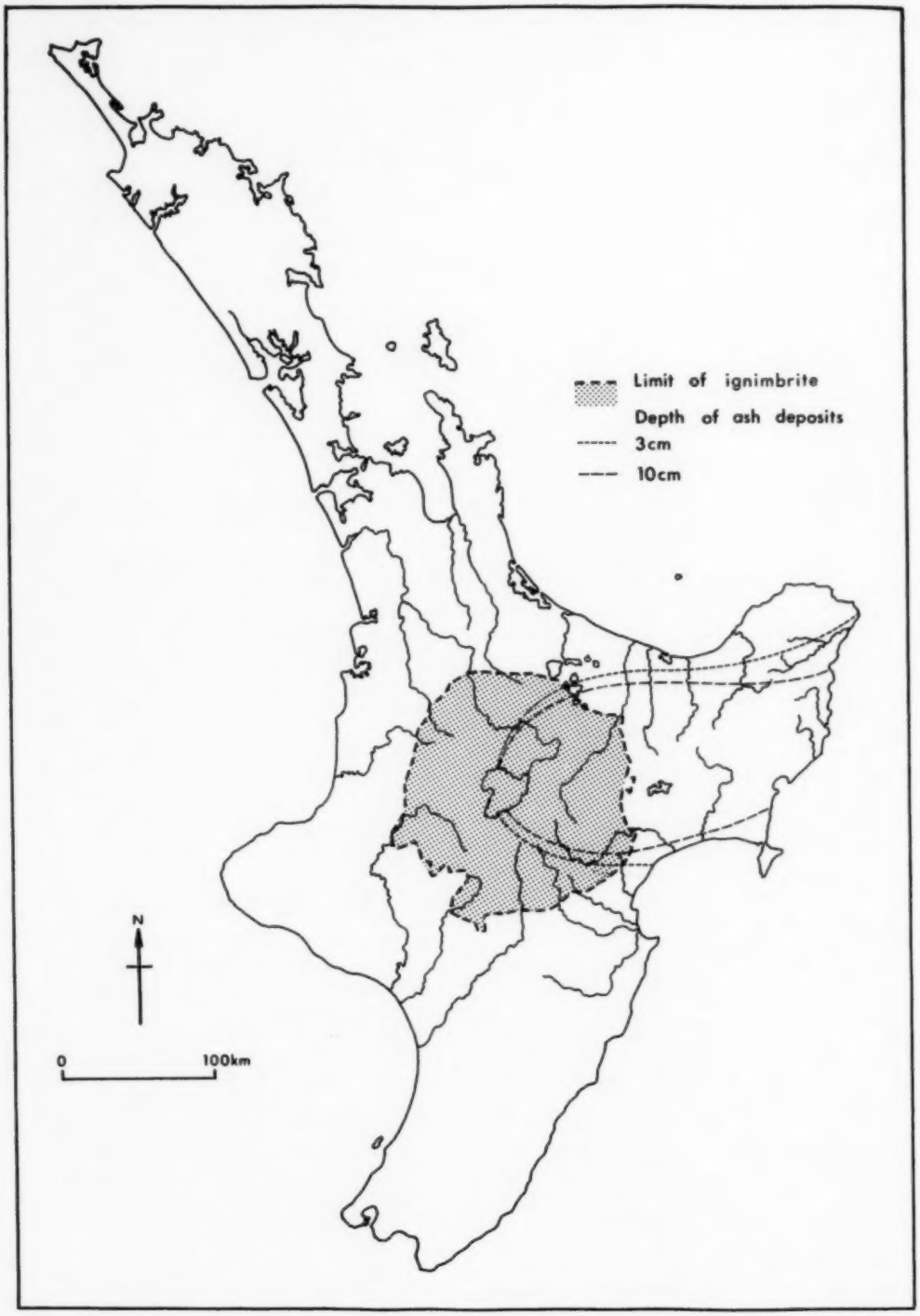

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Fig. 7. Distributions of three non-diadromous fish species and one non-diadromous crustacean species in relation to ash deposition, North Island, New Zealand. (A) Cran's bully (*Gobiomorphus basalis*). (B) Dwarf galaxias (*Galaxias divergens*). (C) Brown mudfish (*Neochanna diversus*). (D) Koura (*Paranephrops planifrons*).

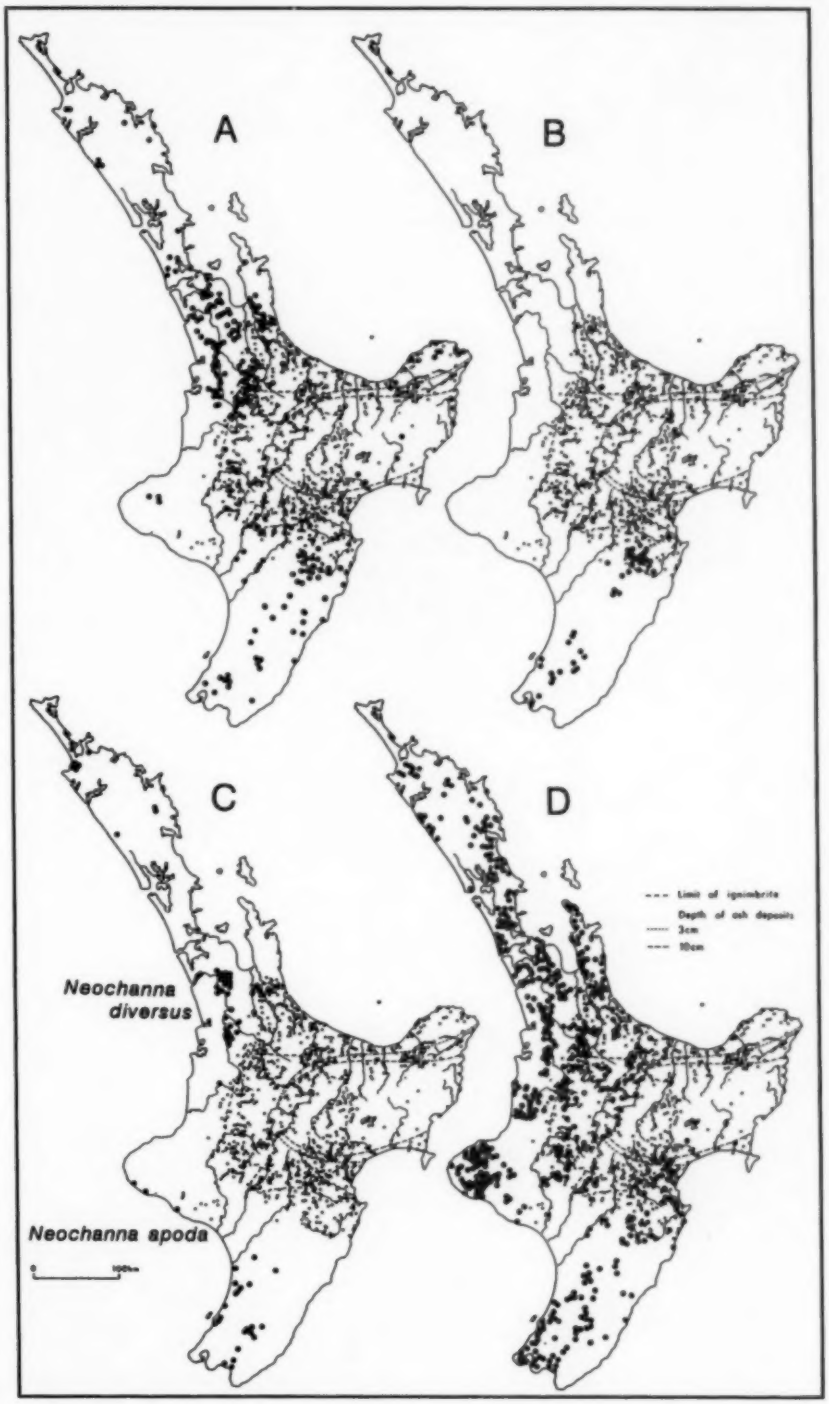

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Fig. 8. Distribution of longfinned eel (*Anguilla dieffenbachii*) in relation to ash deposition, North Island, New Zealand.

as Okarito), are absent from more southern catchments (including and south of the Waiho River, which is where glaciation was most intense and where glaciers still extend to low elevations). Some non-diadromous species, such as dwarf galaxias (*Galaxias divergens*) and upland bully (*Gobiomorphus breviceps*) have not spread southwards into the glaciated zone at all (Figs. 10A and 10C), but others have, though not far down the West Coast. As was the case with the scenario involving volcanism in the eastern North Island, patterns of distribution of invertebrates with nonflighted adults should be consistent with those of non-diadromous fish. Comparable data are not available for these invertebrates except, once

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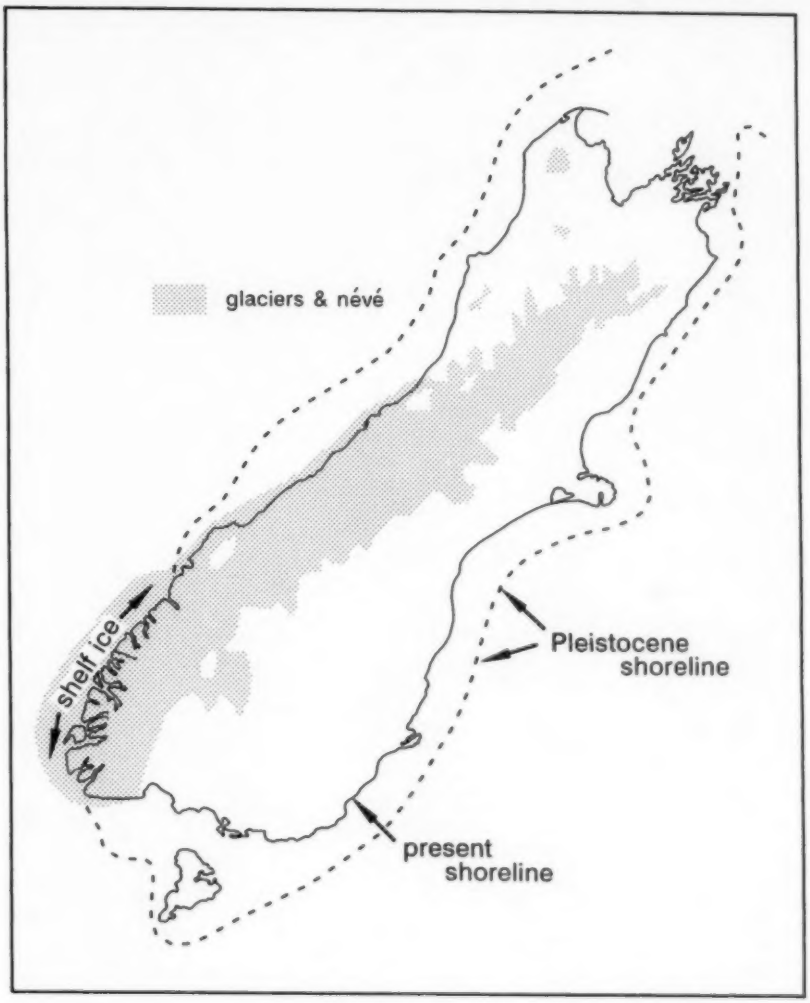
Fig. 9. Ice sheets in South Westland, South Island, New Zealand during Pleistocene glaciation (after Fleming 1979).



more, for koura (*P. planifrons*), which is very largely absent from the same area as non-diadromous fish are absent in southern West Coast catchments (though there is a population in the Waita River catchment, perhaps a relict that survived glaciation) (Fig. 10D).

It is thought that there were some unaffected refugia in places along the West Coast, and possibly brown mudfish and koura (both non-diadromous; Figs. 10B and 10D) retained a distribution to the south using these refugia. It is perhaps no coincidence that both species can live in isolated pools without the need for flowing water; moreover, brown mudfish can survive in ephemeral habitats that become dewatered for several months (McDowall 1990).

In contrast with non-diadromous species, most diadromous fishes are widespread and quite speciose in these more southern catchments, e.g., longfinned eel and banded kokopu (*Galaxias fasciatus*; Figs. 11A and 11B). They can be assumed to have invaded these river systems once the ice retreated and habitat conditions became tolerable.

Here again is a scenario that shows repopulation of perturbed, and probably defaunated, habitats by diadromous fish. A general pattern seems clear, and this generality ought to be applicable more widely.

Diadromy in boreal North American freshwater fishes

The proportion of species in the North American freshwater fish fauna of boreal coastal drainages that is diadromous is only a little lower than in New Zealand. However, this does not mean that fewer boreal North American species are diadromous and many are. The slightly lower proportion of diadromous species is due to there being a richer fauna of non-diadromous species, much of it of central North American - Mississippian derivation, that has moved up into the United

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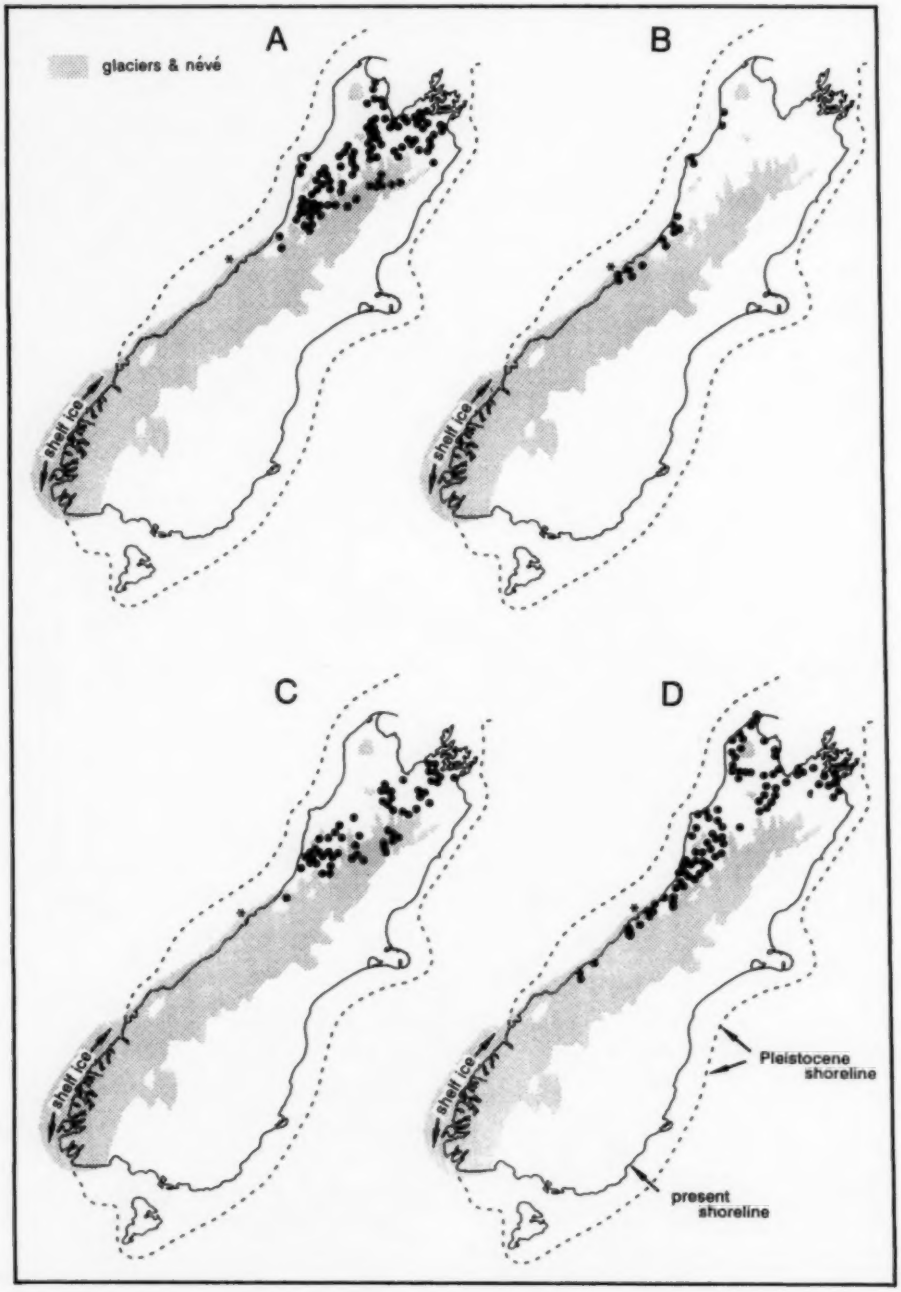
Fig. 10. Distribution of non-diadromous species on the West Coast of the South Island in relation to the presence of a late Pleistocene ice sheet. (A) Upland bully (*Gobiomorphus breviceps*). (B) Brown mudfish (*Neochanna apoda*). (C) Dwarf galaxias (*Galaxias divergens*). (D) Koura (*Paranephrops planifrons*).



States and Canada and has spread coast wards following glacial retreat (Scott and Crossman 1973; Crossman and McAllister 1986; Lindsey and McPhail 1986; McPhail and Lindsey 1986; Robison 1986; Underhill 1986). An analysis of the freshwater fish faunas of the Atlantic and Pacific seaboards of North America (McDowall 1988) showed that in any 1° latitudinal band upwards of 15 diadromous species are present at latitudes around 40–45°N on the Atlantic coast, and that

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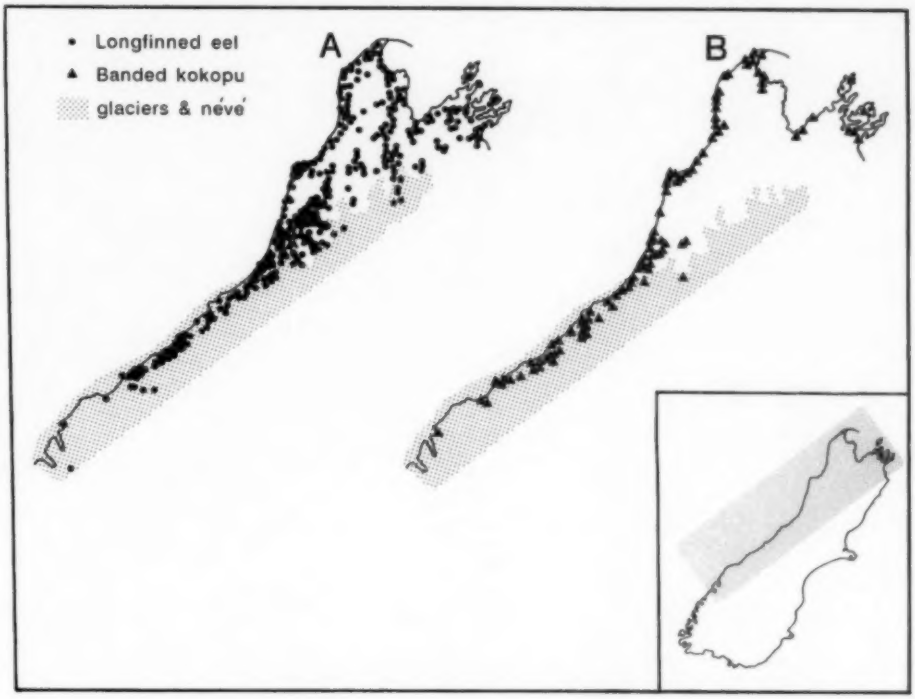
Fig. 11. Distribution of representative diadromous on the West Coast of the South Island in relation to the presence of a late Pleistocene ice sheet. (A) Longfinned eel (*Anguilla dieffenbachii*). (B) Banded kokopu (*Galaxias fasciatus*).



diadromous species may comprise 30–50% of the fauna towards 60°N (Fig. 12). Along the Pacific coast, upwards of 20 species are diadromous around 60°N, and more than about 15 species at 40–70°N; again, up to 50% of the fauna may be diadromous (Fig. 13). Along both coasts, a high proportion of these species is salmonids and osmerids, but there are also clupeids and basses (especially along the Atlantic coast), lampreys, sturgeons, and an array of other species. Thus, about as many species are diadromous along boreal coasts of North America as are diadromous in New Zealand; therefore, diadromy should be a significant factor in explaining patterns of distribution of species, their inland penetration and relative abundance, and in their role in the structuring of freshwater fish communities and the restoration of fish populations to perturbed habitats.

The situation along boreal coasts of North America differs from that in New Zealand in that North American diadromy is nearly always anadromy, whereas in New Zealand the majority of species is amphidromous. This difference essentially means that, in North America, most of the fish migrating up rivers from the sea are mature adults, usually of substantial size, whereas in New Zealand most of them are juveniles that are small (usually less than about 70 mm and often less than 30 mm). While it might be easy to conclude that North American diadromous species will have greater ability to move upstream, this is a half truth. Some North American diadromous species, on account of their large size and powerful swimming abilities, have great endurance, and are adept at migrating upstream for great distances. They can pass substantial falls in large rivers by leaping. However, they are prevented from moving upstream by steep and high falls especially in small streams. New Zealand's diadromous species, by contrast, as they are not powerful swimmers nor can they jump, are hindered from moving up stream by powerful falls in large rivers; however, they can move upstream very effectively, typically by leaving the water and wriggling up the wetted perimeters of falls that may be several tens of metres high (McDowall 1990), a feat that eludes the largest, most powerful-swimming salmonids. As well, their upstream movement may be a long-term, feeding migration over many months to years so that energetics considerations, important for the nontrophic migrations of salmons and shads, are not really relevant. This is a habit well recognised in eastern North America for the American eel (*Anguilla rostrata*; see Liew 1982).

Since a significant number of boreal North American freshwater fishes is diadromous, this ought to be reflected in their patterns of distribution and in the way fish faunas are re-established in coastal catchments following defaunation or perturbation. Examination of accounts of faunal histories of some areas supports this contention.

Postglacial invasion of boreal North American rivers

There are several situations in boreal North America where there have been investigations of postglacial recolonization by fish of formerly ice-covered habitats.

Milner (1987) and Milner and Bailey (1989) have exam-

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Fig. 12. Occurrence of diadromous and non-diadromous fishes by latitude along the Atlantic coast of North America.

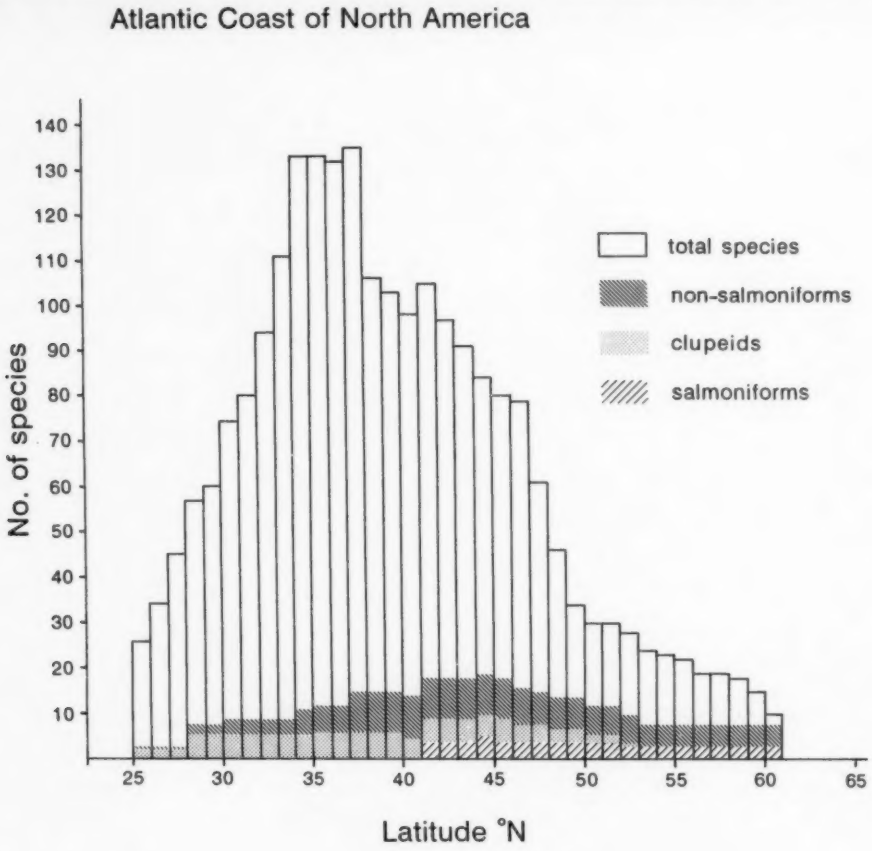
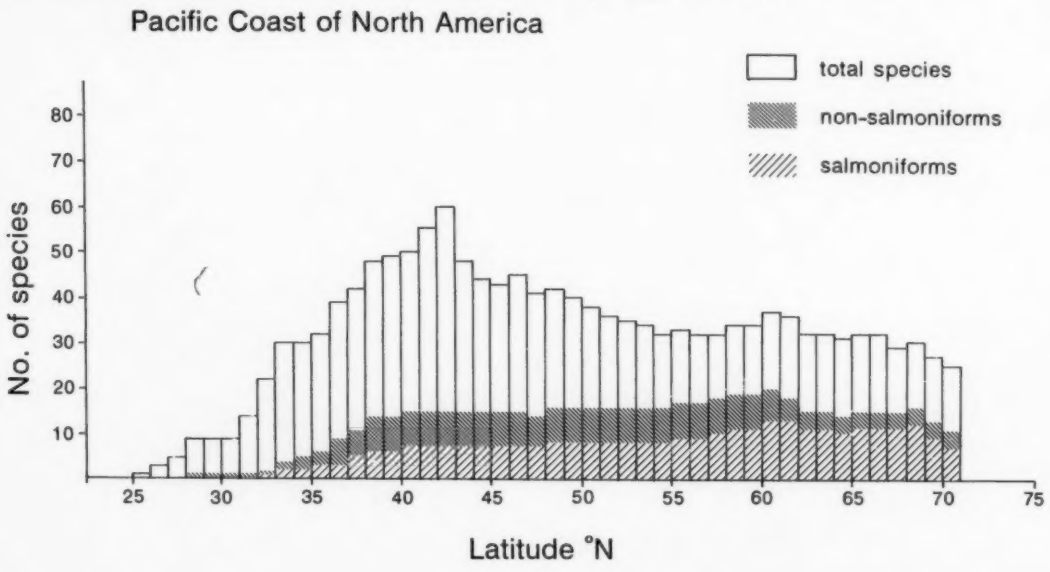


Fig. 13. Occurrence of diadromous and non-diadromous fishes by latitude along the Pacific coast of North America.



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ined the colonization of streams that have been developing in Glacier Bay National Park, Alaska, as glaciers retreat. They found that following establishment by various aquatic insects, recolonization by fish was of salmonids and sticklebacks (Gasterosteidae), in all instances diadromous species.

Hammar (1987) examined postglacial recolonization of rivers of Newfoundland and showed that the fish fauna there consisted of four salmonids, an osmerid smelt, a stickleback (all anadromous). and an anguillid eel (catadromous). The widespread process of establishment of landlocked populations of diadromous species, often a precursor to speciation and the establishment of non-diadromous derivative species (McDowall 1988), was observed for several of the species in Newfoundland. However, with the exception of these landlocked stocks, the entire fish fauna of the island is diadromous, and a role of migration through the sea, in establishing this fauna following glacial retreat, can be identified.

Power et al. (1973) analysed postglacial colonization of the Matamek River, Quebec, and remarked on the difficulty that fish had in "colonizing a small northern river basin." They referred to a "marine route of entry" and, though they noted that all species in the river were "euryhaline," they did not draw the distinction of whether or not they were diadromous, i.e., whether or not they have regular marine stages and explicit marine-freshwater migrations in their life cycles. According to my analysis, the fauna of the Matamek includes the following: three salmonids, one osmerid, one clupeid, one stickleback, and one gadid (all anadromous); and one anguillid eel (catadromous); whether the ninespine stickleback (*Pungitius pungitius*), also present in the Matamek, is anadromous rather than a facultative, euryhaline wanderer through coastal seas, needs clarification. Four additional species that occur there include another non-diadromous stickleback, a non-diadromous catastomid (Catastomidae) and sculpin (Cottidae), and a flounder (Pleuronectidae) that is probably catadromous.

Power et al. (1973) attempted to order the arrivals of fish back into the system as the ice retreated, doing so by determining how far upstream species were distributed in relation to former elevated sea levels penetrating up the river valley and the presence of falls that now obstruct upstream migration. On this basis, the first three species said to have occupied the postglacial river were anadromous, viz. Arctic char (*Salvelinus alpinus*), rainbow smelt (*Osmerus mordax*), and threespine stickleback (*Gasterosteus aculeatus*) (which presumably have all forsaken their anadromous lifestyle in these upper reaches, since the falls are considered a total barrier to upstream migration), plus the ninespine stickleback. They considered that the next arrivals were brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*), both also anadromous. However, this dating system depends on an assumption that all the early colonizing species were equally capable of forsaking their anadromy, and this may not have been the case. The species that are now isolated in the Matamek upstream above falls may well have been amongst the first colonizers. However, other species may have been there just as soon as Arctic char, etc., but because of their need for a return to the sea in every individual's life cycle, they would increasingly have become restricted to reaches downstream of impassable falls that emerged as sea levels dropped, as for instance the American eel, which is not facultatively diadromous and which may not be able to invade the river upstream of the falls. There may be other reasons for considering the eel a later immigrant, such as its being less tolerant of low temperatures and, therefore, not spreading this far north until well after glacial ice had retreated. However, its absence and the absence of other diadromous species upstream of falls is not necessarily evidence of late colonization. It may simply be evidence that diadromy (a return to the sea at some life stage) is obligatory.

Power et al. (1973) also discussed species absent from the Matamek, and in nearly all instances, those that they thought ought to be present (on the basis of habitats available and their presence in nearby rivers also draining into the Gulf of St. Lawrence), were non-diadromous. An exception is the facultatively anadromous lake whitefish (*Coregonus clupeaformis*). However, Black et al. (1986) suggested that this species invaded the Labrador region via an inland route from Quebec rather than from a coastal-Atlantic refugium, and this interpretation would explain the species' absence from the Matamek.

Legendre and Legendre (1984) identified two distinct patterns of postglacial invasion of Quebec. This involved dispersion of stenohaline (i.e., non-diadromous) species from contiguous land areas and river systems to the west and south, as well as invasion of coastal rivers from the sea by euryhaline (about equivalent to diadromous) species. Black et al. (1986) examined similar issues along the northeastern seaboard of Canada (Labrador), and they attributed the presence of a variety of species in Labrador, all of them diadromous, to dispersal through the sea. These included Arctic char, brook trout, Atlantic salmon, rainbow smelt, American eel, and threespine and possibly ninespine sticklebacks. Populations of Atlantic salmon in Ungava Bay rivers were also explained by Black et al. (1986) in this way. By contrast Legendre and Legendre (1984) argued, on several grounds, for dispersal across inland routes. These grounds included the absence of Atlantic salmon from rivers draining northern coasts of Ungava Bay, their absence from Hudson Bay, the failure to find that any salmon tagged around Greenland had returned to the Ungava Bay area, and distinctive behavioural characteristics of the Ungava Bay Atlantic salmon populations.

Black et al. (1986) attributed the distribution of brook trout to both dispersal from Quebec (presumably non-anadromous) and from the Atlantic seaboard (possibly anadromous), though they advanced no explicit reason for this other, perhaps, than that the species is present "throughout Labrador." They considered that rainbow smelt had only recently arrived, though again they did not say on what basis this conclusion was reached. Possibly it was because of its largely coastal distribution, but the fish is largely coastal throughout its range elsewhere on both east and west coasts of boreal North America (Scott and Crossman 1973), apart from populations in the Great Lakes that are introduced (Lawrie 1978). They also thought that ninespine sticklebacks had arrived there recently because of the absence of populations in inaccessible inland locations. As was the case with Power et al. (1973), they attributed the inland presence of some otherwise diadromous species to formerly elevated sea levels facilitating colonization of rivers now above large falls, leading to abandonment of diadromous migrations.

This is an interesting situation, inasmuch as diadromous stocks of some species are highly facultative in their diadromy. Species such as Atlantic salmon and rainbow trout have a small percentage of the fish in each cohort that abandon mi-

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gration and spend their whole lives in fresh water (Northcote 1984; McDowall 1988). Others, like threespine stickleback, seem enormously facultative (McPhail 1992) and seem easily, and often, to abandon diadromy and revert to a wholly freshwater existence. In situations upstream of falls that are inaccessible to fish migrating upstream from the sea, there was bound to have been very rapid selection in diadromous species for nonmigratory genotypes that occur in a minority in populations, as soon as the falls became effective barriers to upstream movement. This is a likely explanation for inland stocks of otherwise diadromous (anadromous) species in such waters, as in the Matamek River (Power et al. 1973) as well as along the Labrador coast (Black et al. 1986).

Much of the discussion of sources from which dispersal of fish into boreal North America took place involved identification of glacial refugia, specifically a Mississippi refugium and an Atlantic refugium. Such refugia were bound to be of critical importance as sources for fishes confined to fresh water, which were not free to move latitudinally with changing climates, and in association with advancing or retreating ice sheets, unless river systems flowed in the same directions, as the Mississippi did (Mahon 1984). Legendre and Legendre (1984) also pointed to a network of interconnecting river headwaters in Quebec that also would have facilitated dispersal and invasion of the postglacial boreal landscape. However, in the case of diadromous species, the concepts of riverine refugia and interconnecting river headwaters seem less relevant. Why, for instance, are McPhail and Lindsey (1986) insistent that the Columbia River was a refugium for diadromous species? It may have been, but need not have. Diadromous fish should be seen as being a sea-dispersing species or gene pool that is enormously flexible in distribution, so that such species may shift their geographical range as easily as terrestrial birds and mammals, and probably did so through the sea along both coasts of North America during the Pleistocene, driven or facilitated by climatic coolings and warmings. Diadromous species would have been able to invade rivers and lakes, almost as soon as habitats became tolerable, by the dispersion of sea-living stages, just as has been shown by the present day by the work of Milner in streams of Glacier Bay, Alaska (Milner 1987; Milner and Bailey 1989).

Similar scenarios can probably be described for lake or river migratory species in the Great Lakes. Particularly as a few normally diadromous species gained access to the lakes after glacial retreat, those species that were facultatively diadromous would have established migration patterns involving the lakes and their inflowing rivers. Since human modification of the drainage patterns, additional diadromous species, like alewife, shad, and sea lamprey have gained access to the lakes and this scenario has been repeated (Smith 1968), and it has recurred in a third set of circumstances as human liberations of diadromous species of Pacific coast salmonid have been undertaken (Lawrie 1978; Kwain 1987).

Species richness along the Pacific coast

McPhail and Lindsey (1986) and Lindsey and McPhail (1986) commented on the sparseness of the freshwater fish fauna of the Pacific coast drainages of North America, there being only 61 species in the area from the Columbia River north to the Stikine, and 69 species in rivers north of the Stikine. The impoverishment of these faunas presumably is due in some measure to widespread extirpation of fishes in Pacific coastal drainages by Pleistocene glaciation, and the difficulties encountered by the Mississippian fauna in reinvading these drainages from the east after climatic amelioration and glacial retreat. McPhail and Lindsey seemed to recognise no explicit role for diadromy in facilitating the return of fish species to these river systems once the ice did retreat, yet it seems inevitable that the scenario that Milner (1987) and Milner and Bailey (1989) described on a very small scale in Alaska also took place on a much greater temporal and geographical scale along the entire Pacific coast of North America where there was an impact from glaciation. Such a wider scenario seems likely to have involved diadromous species retreating southwards, in part driven by ice sheets covering the land but in part undertaken by fish species that increasingly encountered acceptable temperature regimes in more southern rivers where they are no longer present because temperatures there now are higher than their tolerances. I speculate that, as climate oscillated between glacial and interglacial periods, distributions of diadromous fish would have moved south and north, being driven by or following the advances and retreats of ice sheets and cool temperatures. Each species is likely to have occupied a latitudinal band along the coast, dictated largely by temperatures, that is perhaps comparable in latitudinal range to that now occupied, though at different and varying latitudes. What we see today is a major retreat of ice sheets accompanied by a northward advance in the distributions of diadromous fish. For such species, the concept of refugia in various specific coastal river systems seems to have little relevance since they have a facility for moving latitudinally with changing climate. Whereas the non-diadromous fauna of the region is impoverished presumably owing to the impacts of glaciation, it seems likely that glaciation had minimal impact on the diadromous fauna that moved latitudinally as either forced or facilitated by climatic conditions. There seems little reason to regard the diadromous fauna as impoverished, and the higher proportion of diadromous to non-diadromous fishes in the Pacific coast fauna can be explained by two facts: (*i*) Non-diadromous fishes were extirpated along the coast by glaciation, had difficulty reinvading the coastal drainages from Mississippian refuges following glacial retreat, and are now less speciose than faunas elsewhere; (*ii*) Diadromous species moved latitudinally during climatic oscillations and suffered little glaciation-driven extirpation, and retain their former species diversity.

The other edge of diadromy's sword

There are two distinct sides to the role of diadromy in determining distribution patterns. On one hand, as discussed above, diadromy facilitates dispersion of species around coastlines and provides access up rivers from the sea to allow invasion of new, or reinvasion of formerly perturbed, riverine and lake habitats; thus, when a diadromous species is extirpated from a river system, its return there is usually assured by dispersion through the sea from nearby river systems where perturbation has not occurred or has been less severe. On the other hand, diadromy and the need to migrate upstream from the sea into fluvial habitats means that such fish are excluded from freshwater habitats upstream of hindrances to migration. Moreover, diadromous species vary in both their instinctive drives to

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move upstream as well as their ability to migrate past hindrances to migration (McDowall 1993), hindrances that vary from simply distance and elevation, through swift rapids, to torrents, falls, and in modern times polluting discharges and human-constructed weirs and dams.

Natural patterns of distribution thus reflect the impacts of these hindrances, and new perturbations may result in the exclusion of diadromous species from otherwise suitable habitats because fish passage is obstructed. This is seen with great clarity in all lands where rivers have been impounded. In New Zealand, anguillid eels and various galaxiids are excluded from waters upstream of some dams (McDowall 1990). In Spain, where more than 1000 large dams are documented, every diadromous species is endangered (Nicola et al. 1994). The impacts of dam construction on Pacific salmon (*Oncorhynchus* spp.) migrations in the Columbia River are widely known (Netboy 1980) and are repeated in many other rivers in the Pacific Northwest where distributions and access have been widely disrupted and local fish stocks extirpated, as in the Sacramento River by the Shasta Dam (Cope and Slater 1957). Similarly, migrations of Atlantic salmon as well as various shads (*Alosa* spp), sturgeons (*Acipenser* spp.) and others have been impeded and the stocks have declined in rivers in eastern North America (such as the Connecticut River; Taubert 1980). The same is true in the British Isles (reviewed in McDowall 1988). Diadromous species in the Meuse River in Belgium are drastically reduced (Houvenhagel 1987). Weirs across the great rivers of the Indian subcontinent have greatly reduced runs of *Hilsa* shads. These are examples of a pattern that is almost worldwide, of decline in diadromous species as a result of dam construction that hinders migration. There are thus two distinct sides to the implications of diadromy to both natural fish distribution patterns and their response to perturbation.

Some implications for management

Restoration of fish faunas to aquatic ecosystems following perturbation and extirpation is a natural concern for responsible water and fisheries managers in all parts of the world. While such damaging events are to be discouraged, there are scenarios in both New Zealand and North America that suggest that, with the quite small but biologically and economically important group of diadromous fish species, natural patterns of dispersion and migration are likely to lead to natural restoration of fish stocks once factors causing perturbation have ameliorated or disappeared. This natural restoration has several advantages: (*i*) It happens rapidly, as soon as habitat conditions are again appropriate; (*ii*) It results in stocks that are well adapted to conditions, both the habitats that become available and in relation to migratory patterns and cues that are critical to ensuring the fish are capable of navigating back to rivers from the sea; (*iii*) By no means least, such restoration costs nothing.

Natural restoration ought never to be a substitute for ensuring that there is no perturbation and extirpation, in the first place, but it is the best alternative.

Acknowledgements

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Impacts of logging in Carnation Creek, a high-energy coastal stream in British Columbia, and their implication for restoring fish habitat

G.F. Hartman, J.C. Scrivener, and M.J. Miles

Abstract: The land form, surficial geology, and hydrometeorology of the west coast of British Columbia cause streams in the region to be highly variable in flow and vulnerable to land-use disturbance. Carnation Creek, a small drainage in this region, was studied intensively for > 20 yr to examine the impacts of forest harvesting. Landslides and debris torrents modified steep slope tributaries and the mainstem of the creek. Bank erosion also altered the stream channel on the alluvial flood plain. These effects were additive in the system and reduced the quality of spawning and rearing habitat for juvenile salmonids. In streams like Carnation Creek, it is necessary to restore some stability to the hill slopes and gullies before attempting fish habitat improvements in the main channel. Salmonid production was limited by combinations of processes and conditions that were different for each species and life-history stage. Knowledge of the processes that limit fish production must be applied in habitat improvement work or the projects risk failure. Programs intended to restore natural function to systems or to improve habitat for fish must be planned, evaluated, and reported methodically if they are to succeed and provide information of use to future programs.

Résumé : Sur la côte de Colombie-Britannique, le relief, la nature des dépôts meubles et les facteurs hydrométéorologiques font que les petits cours d'eau ont un débit très variable et sont facilement perturbés par l'utilisation du territoire. Les impacts de l'exploitation forestière sur le ruisseau Carnation, qui draine un petit bassin-versant de la région, a été étudié intensivement pendant plus de 20 ans. Les glissements de terrain et les torrents de débris ont modifié les tributaires à forte pente et le tronc principal du ruisseau. De plus, l'érosion des berges a modifié le chenal du cours d'eau dans la plaine alluviale. Ces facteurs ont eu des effets additifs sur le système et ont réduit la qualité des frayères et des aires d'alevinage des salmonidés. Dans le cas d'un cours d'eau comme le ruisseau Carnation, il est nécessaire de rétablir une certaine stabilité des pentes et des ravins avant d'essayer d'améliorer l'habitat des poissons dans le chenal principal. La production de chaque espèce de salmonidé était limitée par une combinaison particulière de processus et de conditions. Une connaissance des processus limitant la production des poissons doit être appliquée aux travaux d'amélioration des habitats, qui risquent autrement d'échouer. Les programmes visant à rétablir la fonction naturelle des systèmes ou à améliorer l'habitat des poissons doivent faire l'objet d'une planification, d'une évaluation et de rapports méthodiques, si on veut qu'ils réussissent et produisent des données utiles pour les programmes à venir.
[Traduit par la Rédaction]

Introduction

Drainage basins of the west coast of British Columbia hold high resource values for forestry, fisheries, wildlife, tourism, and cultural heritage. The significance of the fisheries and forestry values within the drainages has been recognized for decades, and conflicts regarding the impacts of forest management activities on fisheries resources date back to the 1950s. While managing a high level of use of resources that share a common land base is challenging in itself, the situation in coastal drainages of British Columbia is made more difficult because they are located in mountainous terrain with shallow and unstable surficial material. Coastal drainages are also subject to high precipitation and severe storms, which cause hydrological regimes that vary with watershed size and elevation. Flow regimes in small and low-elevation streams are driven by winter rain, while those of higher elevation are driven by winter rain, rain on snow, and spring snowmelt events. Regimes may differ from one drainage to another, but in all cases the high hydrological energy, the extremely flashy nature of these streams, and the transport of sediment are key elements in the challenge of managing fisheries and forestry resources. These conditions also make watershed restoration and stream habitat improvement difficult.

In this manuscript, we use "restoration" to describe activities that attempt to return disturbed drainage basins to near predisturbance condition. "Habitat improvement" refers to specific efforts within the stream channel and riparian zone to enhance spawning, rearing, or feeding conditions for fish.

The impacts of forest management activities on stream ecosystems are complex and vary in timing and duration, depending on system type, forestry activity, and fish species present. The major groups of physical and biological processes studied

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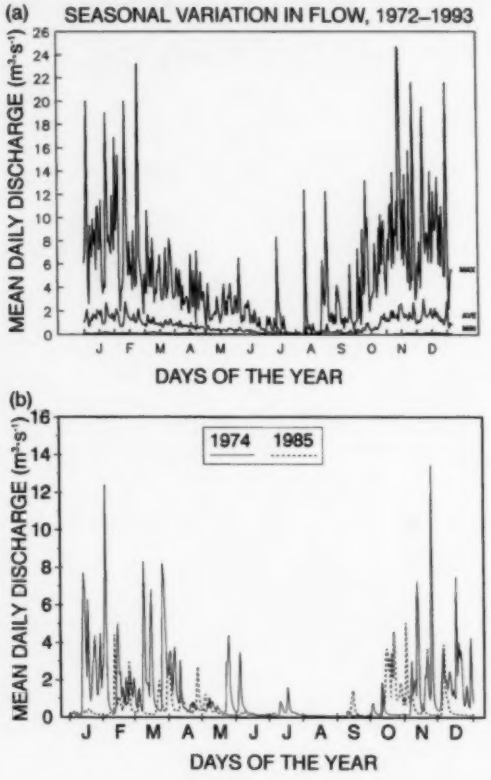
Fig. 1. (*a*) Daily variation of stream flow at B-weir in Carnation Creek, 1972–1993. (*b*) Mean daily flows during an example of a wet year, 1974, and a dry year, 1985.



at Carnation Creek included hydrological, fluvial-geomorphological, thermal, and trophic processes. Five generalizations emerged during the project:

(1) The processes were extremely complex and almost fully interconnected (Hartman and Scrivener 1990).

(2) Each species and life stage of salmon and trout responded differently to the impacts of forestry activities.

(3) Responses differed geographically. Watershed orientation or topography affected impacts. Some responses occurred ≥ 4 km downstream from the location of logging impact (Hartman et al. 1987; Meehan 1991).

(4) Responses differed in duration. Some persisted for a few years, while others continued longer than originally expected (Scrivener and Brown 1993) and may continue for centuries (Meehan 1991).

(5) Impacts of forestry activities may combine with conditions in the marine environment to limit fish population numbers (Hartman and Scrivener 1990).

In this paper we examine the implications of these generalizations to watershed restoration and stream habitat improvement programs.

To improve fish habitat, it is necessary to understand how various structures or in-stream improvements can affect the various life stages and species. Any primary limiting factors must also be understood for the species being enhanced. This paper illustrates the nature of some of the limiting factors for species in Carnation Creek and comments on how biologists determine limiting factors for habitat improvement projects. Terrain, hydrology, and stream productivity are also important elements that, over time, have influenced the evolution of successful life history strategies for a population. Enhancement should be tailored to limiting factors and life strategies of the target population.

The stream ecosystem: Carnation Creek

Physical conditions

Carnation Creek is ~8 km long and drains an area of 10 km^2. It is located in the Barkley Sound region of Vancouver Island. The bedrock consists principally of the Vancouver Island Intrusion, a Jurassic age batholith of granodiorite. Surficial materials are tills and colluvium that are frequently only thin veneers overlying bedrock (Jungen, no date; Alley 1975).

The terrain is steep and rocky and forested with western red cedar, coastal western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and red alder (*Alnus rubra*). Above 5 km from the mouth, the stream flows through a bedrock-controlled channel. Elsewhere, it passes through a 100–300 m wide alluvial flood plain, except for a short canyon reach, 3.1–3.5 km from the mouth. Before logging, channel structure was controlled by large woody debris (LWD) and by stream banks with erosion resistant vegetation. The amount, type, and role of LWD was described by Toews and Moore (1982), and the responses since logging were described by Powell (1988). Side-channel and tributary areas on the alluvial plain were characterized by Brown (1987).

Carnation Creek is, hydrologically, a high energy system. From 1970 to 1990, ~95% of the 210–480 cm annual precipitation occurred as rain, and most of it fell during storm events in the period between November and April (Hartman and Scrivener 1990). Stream flow increased rapidly in response to rainfall within storms whether they occurred during summer or winter (Fig. 1*a*). Because soils were saturated, water moved quickly to bedrock in the coarse shallow soils, and the ephemeral channel network expanded rapidly up the slopes (Hetherington 1982, 1995). Quick runoff was further enhanced by movement of water through soil macrochannels (subsurface channels left by decomposed tree roots). Because of these climatic and geological features, the stream reached flood levels within a few hours and water levels declined as rapidly after storms (Fig. 1*a*).

Minimum stream flows occurred during the summer months, although storms and high discharges could occur during any month (Fig. 1*a*). Large differences occurred between wet and dry years (Fig. 1*b*). Discharges, in summer, were low during both wet and a dry years, but the volume of discharge and the frequency of events with flows <2 m^3·s^{-1} were much greater during a wet year, 1974, than a dry year, 1985 (Fig. 1*b*).

Streams on the west coast of British Columbia are usually low in biological production because of nutrient, light, and

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Fig. 2. Schematic representation of the freshwater life histories of juvenile chum, pink, sockeye, chinook, and coho salmon and steelhead and cutthroat trout for as long as 5 years.

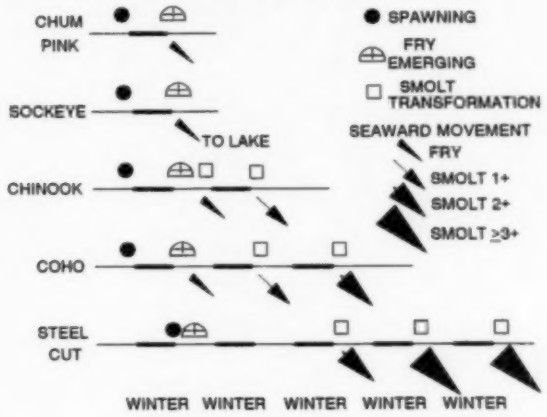
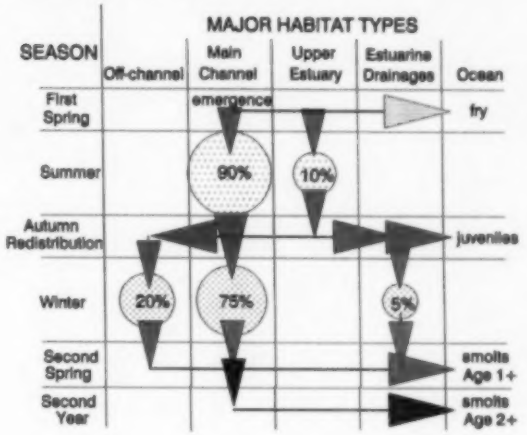


Fig. 3. Major habitat types and life history strategies that are used by coho salmon in Carnation Creek.



temperature conditions. In Carnation Creek, conductivity, an indicator of productivity, was low (20–60 μmhos·cm^{-2}) and inversely related to stream flow (Scrivener 1988). Bedrock did not weather rapidly to release minerals, and those released were flushed rapidly through the watershed. Only 24–47% of the total light available reached the stream under the old-growth forest (Shortreed and Stockner 1982). Therefore, stream autotrophic production was limited by low levels of light and nutrients, especially phosphate (Stockner and Shortreed 1976). Stream temperatures averaged only 9–11°C from May to September (Holtby 1988).

Fish populations

The fish fauna in Carnation Creek consists of coho and chum salmon (*Oncorhynchus kisutch* and *O. keta*), steelhead and cutthroat trout (*O. mykiss* and *O. clarki*), and two species of cottids (*Cottus aleuticus* and *C. asper*). The salmonid species demonstrate a variety of alternative life-history strategies (Fig. 2), the advantages and disadvantages of which are discussed.

Chum salmon limit their freshwater life to spawning and incubation stages (Fig. 2). They spend their full postembryonic growing period at sea, in an environment far more productive than that of their natal stream, but they are subjected to greater potential predation pressures in the ocean. Their reproduction is concentrated in the lower reaches of the stream. Thus, populations are at risk from the impact of major habitat disturbances such as elevated sediment loads and temperature regimes that reach lower parts of the stream. These disturbances have cumulative downstream effects that impact incubation success and marine survival (Scrivener 1991).

Juvenile coho salmon exhibit five different life history strategies in Carnation Creek (Fig. 3). They may hatch and rear in the main channel until smolt transformation at age 1+ or 2+ (Hartman and Scrivener 1990). They may hatch and rear in the main channel before moving, during autumn, into off-channel habitat on the flood plain. Coho fry may disperse downstream during March to June, remain in the estuary until October or November, grow rapidly, and then disperse to sea (Tschaplinski 1987), or move upstream to estuarine drainages (Scrivener and Brown 1993).

The success of a particular coho life-history strategy depends upon conditions in the stream during the winter. For example, during years when late winter and early spring water levels were low, juvenile coho survival and smolt production was low in the off-channel habitat (Brown 1985). Survival was better in the main channel. During winters with many storms, access and survival were high in the off-channel, but low in the mainstem habitat. These different patterns of habitat use provided stability of smolt production and additional options for habitat improvement.

Trout had a 2- or 3-yr residence in the stream (Fig. 2), but fewer habitat strategies than those that coho exhibited (Fig. 3). Steelhead used only the main channel, while cutthroat used some off-channel habitats (Brown and Hartman 1987).

Characteristics of forest management impacts in west coast B.C. streams

Forest management affected the interrelated hydrological-geomorphological, thermal, and trophic processes in Carnation Creek (Hartman and Scrivener 1990). During phase I of the logging, 1976–1981, 41% of the basin was clear-cut. During phase II, 1987–1994, another 42% was cut. To date, ~61% of the length of headwater streams has been logged, requiring 38.5 km of road and 21 crossings of hillslope channels. This activity has caused changes to water routing and, deposition of ~25 480 m^3 of sediment, principally derived from landslides, into the creek (S. Chatwin, B.C. Ministry of Forests, Victoria, B.C., personal communication). The relevance of these changes and associated processes can now be discussed with regard to habitat improvement and restoration within this type of ecosystem.

Hydrological-geomorphological processes

Several changes in hydrological conditions in the Carnation Creek basin have occurred since logging. Annual water yield increased 9–16% following near total clear-cutting of a 12-ha sub-basin (H-tributary; Hetherington 1982), but an increase

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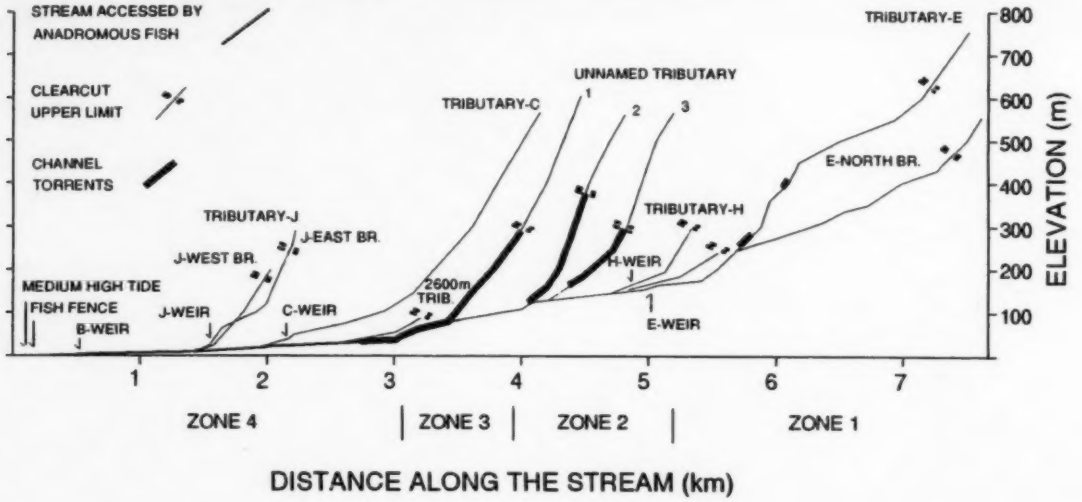
Fig. 4. Gradients of Carnation Creek and tributaries, limits to clearcuts, and locations of debris torrents.



was not detected for the total basin following phase I. Following logging of this sub-basin, summer flow levels increased 78% and runoff peaks increased ~20%, but only for early autumn storms. Alterations of natural hydrological pathways such as loss of water interception by the canopy and compaction of soils along skid trail road, and ditch channels probably caused the increased yield and runoff (E. Hetherington, Canadian Forestry Service, Victoria, B.C., personal communication). After logging, groundwater levels were elevated in some areas of the flood plain, but declined at other locations when compared with control sites.

Hydrometeorological conditions strongly affected slope stability in the Carnation Creek watershed, and both hydrological and sediment transport processes affected structural changes in the stream channel. At Carnation Creek, Caine's (1980) criterion for susceptibility of slope failures was exceeded during rain storms with 2-yr return periods, even at undisturbed sites. Elsewhere in southwestern British Columbia, slope failures and debris torrents[2] have occurred at smaller rainfall intensities than those proposed by Caine (1980) when soil moisture has been increased by previous rainfall or snowmelt (Church and Miles 1987). All of these criteria were exceeded at some logging disturbed sites at Carnation Creek, even at short-duration rainfall intensities (Hartman and Scrivener 1990). The volume of landslide material has increased 12-fold since logging. This is about one third of the increase (34-fold), that was observed for watersheds on the Queen Charlotte Islands (Rood 1984, 1990). This is consistent with information from Swanson et al. (1987) who reported that frequencies of landslides and debris torrents were increased when forestry activities caused elevated water yields and shorter water runoff routes on steep hill slopes.

[2] A debris torrent is a mass movement of water-charged material that flows down a steep, confined, pre-existing stream channel (Swanston 1974; Van Dine 1985). The material includes rocks as large as several meters in diameter and wood, ranging from mulch to large logs.

Two sets of structural change occurred in Carnation Creek, which are temporally and spatially different. Although their effects were cumulative, they were caused by forestry activities in different parts of the basin. First, clear-cutting to the stream margin on the flood plain caused destabilization of LWD, erosion of stream banks, entrainment of sediment, widening of the channel, and deposition of sediment in the lower reaches (Hartman and Scrivener 1990). These events began following a major storm, 3 years after logging was initiated, and they accelerated for a decade. A second set of changes took place 5–8 yr after logging when a landslide occurred in the canyon and debris torrents came down three steep gullies (Fig. 4). These events occurred during a single storm with a calculated 25-yr return period (Fig. 5). There were three large piles of LWD on the banks and ~1500 m^3 of sediment remaining in the channel of Carnation Creek at or near the toe of the torrent.

Many changes occurred in the lower reaches of Carnation Creek after the destabilization of LWD and the large input of sediments. LWD volumes declined 50% within a few years in stream reaches with a clear-cut riparian zone (Toews and Moore 1982) and 0–20% within a decade elsewhere in the channel (Powell 1988). This pattern is typical of coastal streams (Fig. 6). Channel diversity (e.g., pool volumes) and sediment storage are directly related to the LWD volume (Bisson et al. 1987), so the channel became structurally more uniform (pool habitat filled) and stream sediments were more mobile. The additional sediments caused dewatering of some areas, transport of fines into spawning gravel, and disturbance of incubating salmon eggs (Scrivener and Brownlee 1989). Some of this sediment is stored in channels that have been recently abandoned by the stream. Some of it is stored above large LWD jams and then periodically released during storm events. Watershed-restoration and habitat-improvement projects must recognize and understand these multiple source problems and their cumulative effects before fish habitat improvement structures are added to the channel.

Sediment accumulating behind LWD has caused two relo-

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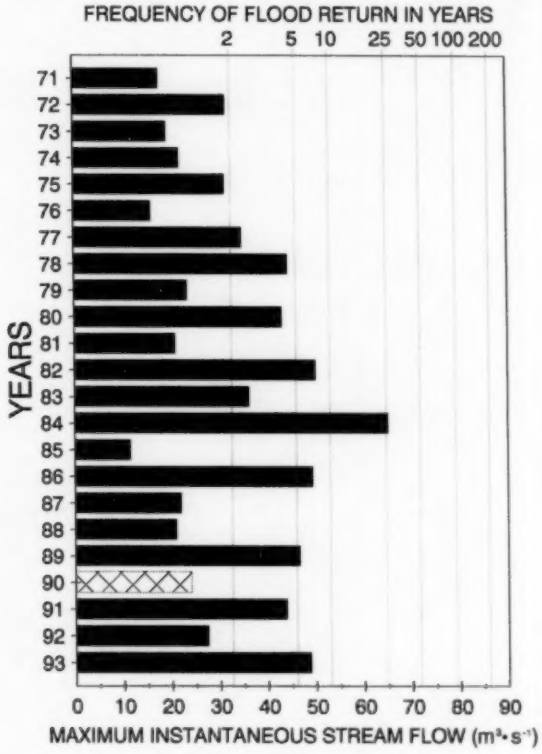
Fig. 5. Annual peaks of stream flow at B-weir and their predicted reoccurrence in Carnation Creek. A Gumbel frequency distribution is superimposed on the graph to show probable return periods for peaks. The 1990 maximum was predicted with a correlation of annual peak flows from B- and E-weir ($R^2 = 0.77$).



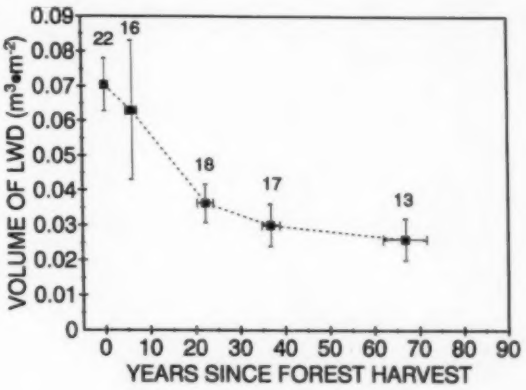
cations of the main channel of Carnation Creek. Gravel filled the old channel at km 1.3 and 1.7 (Fig. 4), and new 150 and 75 m long channels were scoured during 1986 and 1993 storms, respectively. These changes were caused by floods with ~7-yr return periods (Fig. 5). Fish habitat is now ephemeral in the old channels and additional sediment was mobilized when the new channels were formed.

The seven ephemeral tributaries and side-channels, located on the valley floor, were not altered by forestry activities as much as the mainstem of Carnation Creek. There was some deposition of debris and loss of aquatic vegetation within these habitats, but their structure was not altered (Brown 1985).

Thermal processes

Stream temperatures increased 0.5, 0.75, and 3.2°C during winter, spring, and summer, respectively, for the decade following logging of the riparian zone of Carnation Creek (Holtby 1988; Hartman and Scrivener 1990). During summer, elevated stream temperatures occurred when more radiant energy reached the stream. This type of impact has had deleterious effects on salmonids elsewhere (Brown 1971; Hall and Lantz 1969; Hall et al. 1987), but it enhanced fish growth in Carnation Creek (Holtby 1988). Increased stream temperatures during winter and spring caused rapid embryonic development and early emergence of salmonid fry in Carnation Creek (Hartman and Scrivener 1990). This had negative impacts on chum salmon, positive and negative impacts on coho salmon, and positive impacts on age 0+ trout.

Fig. 6. Mean volumes of large woody debris (10 cm diameter) and standard errors for 53 streams on Western Vancouver Island (DFO data, including Carnation Creek), for 6 streams on the Queen Charlotte Islands (from Hogan 1986) and for 27 streams on the Olympic Peninsula, Washington (from Grette 1985; Bisson et al. 1987). The numbers of streams used to calculate the means are also shown.



Trophic processes

Three changes occurred, following logging, that altered trophic conditions in the stream:

(1) The riparian forest was cut for ~2.25 km along the lower 5 km of stream and only a thin line of trees was left on one side of another 1.0 km of stream (Hartman and Scrivener 1990). Leaf litter input from these areas was stopped or reduced.

(2) Sunlight reached the stream and stream temperatures were increased (Stockner and Shortreed 1976; Holtby 1988).

(3) The flux of nitrates through the system was increased, particularly during winter freshets (Scrivener 1989). The increase in total phosphorus was very low.

Logging of streamside areas produced a statistically significant increase in primary production within the stream (Shortreed and Stockner 1982), but the increase was small when compared with other studies (Minshall et al. 1983; Gregory et al. 1987). The elevated stream temperatures and light intensities had little or no influence on algal production in Carnation Creek (Stockner and Shortreed 1976). Primary production was limited mainly by low concentrations of phosphorus. The algae that grew were partially removed by freshets during summer and almost totally scoured away during September and October freshets (Stockner and Shortreed 1976). Prior to logging, production was primarily heterotrophic, given the stream size and functional attributes described by Vannote et al. (1980). The input of leaf litter and its conversion to detritus were the basis for most of the macroinvertebrate production in Carnation Creek (Culp 1988).

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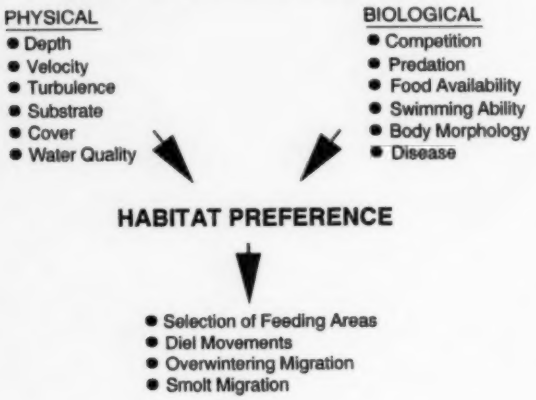
Fig. 7. Physical and biological factors that determine habitat preference for fish, and the biological functions in which habitat preferences are exhibited (Redrawn from Bisson 1989).



The effects of logging on macroinvertebrate production was negative. Densities of seven taxa in summer (three genera of Plecoptera and Ephemeroptera, Chironomidae) and of five taxa during other seasons (two Ephemeroptera, two Plecoptera, Chironomidae) were lower in clear-cut sections than in leavestrip sections of Carnation Creek (Culp and Davies 1983). Total macroinvertebrate densities were reduced 41–50% when compared with densities during the prelogging phase and with densities from unlogged control sites. Culp and Davies (1983) hypothesized that increased transport of fine sediment, reduced stability of the channel, and decreased input of leaf litter were responsible for this effect.

Duration of impacts

Most forest harvesting impacts on streams fall into three duration categories. The first group is related to regrowth of watershed vegetation. In coastal streams, these impacts begin immediately after logging and they continue for 3–20 yrs until hydrological recovery is established and vegetation has begun stabilizing the soils and channels and reshading the stream. Examples are increased stream temperatures when logging allows more sunlight into the stream (Holtby 1988); changed concentrations of nutrients and dissolved ions in stream water when soil disturbance (slash burning, herbicides) permits more leaching of soils (Scrivener 1988, 1989); increased fine sediment when slope soils, road cuts, road surfaces, and road ditches are exposed to erosion (Beschta 1978); and decreased stream detritus when riparian vegetation is removed (Culp and Davies 1983). The second group of impacts does not begin immediately, but initiation depends on the occurrence of large flood events with 5- to 10-yr return periods (Fig. 5) or the deterioration of stump root strength, which occurs 3–5 yr following logging (Swanston 1974). Impacts accelerate for a decade and may persist for several decades. Examples include increased sediment production from hillslope failures and gully torrents (Fig. 4); increased erosion and transport of sediment and bedload when streambank integrity is lost (Hogan 1986; Scrivener and Tripp, in press); reduced streambed stability and channel diversity when more sediment enters streams (Powell 1988); and changed composition of spawning gravel when sediments are transported from upstream channels (Scrivener and Tripp, in press). The third group contains very long-term impacts that appear 10–20 yr after logging, and they continue throughout the forest rotation. An example is the structural and habitat changes caused by the loss of LWD in streams, which occurs over a long period in time (Fig. 6). Three centuries may be required before volumes of LWD recover in coastal streams (Gregory et al. 1987).

These comments show that restoration or habitat improvement programs may have to be of different duration depending upon the physical problem being treated. In some cases there may be no "quick fixes" for altered habitats, and it may be necessary to wait for natural recovery to begin before initiating treatment.

Impacts that limit populations

Identifying limiting factors

Many physical and biological features influence the abundance of salmonid populations and it is crucial to identify the factors that limit production (Reeves et al. 1991). There may be specific daily or seasonal periods relating to food, cover, water quality, or predation that control the size of a specific population. Examples include maximum daily stream temperature during summer, limited spawning habitat during autumn, and limited rearing habitat during winter. Therefore, we must understand how limiting factors might operate on a population and restoration and habitat improvement measures must focus on such factors, if they are to be successful (Koski 1992; Hall and Baker 1982; Everest and Sedell 1984; Bisson 1989).

In some cases a single factor may limit production. Examples include the absence of spawning habitat, the existence of barriers, or some form of serious habitat damage. In these circumstances, treatment of a single factor is appropriate. For example, in ~20 British Columbia projects, gravel placement has provided spawning habitat where little or none previously existed (Hartman and Miles 1995).

In most cases it is an oversimplification to attribute population limitation to a single factor. Overall abundance of a population is a reflection of the way the animals respond to the total environment. Several physical and biotic factors, acting alone or in concert, can potentially limit production (Bisson 1989). They shape habitat preference, determine patterns of behaviour (Fig. 7), and ultimately affect annual production levels. Habitat improvement projects must identify the major conditions and associated processes, from within a model of the type shown in Fig. 7. Bisson (1989) stressed that pitfalls can be minimized when doing a limiting factor analysis by obtaining (1) knowledge of the life histories of the species present, (2) detailed and accurate habitat inventory information of the area, (3) an appreciation of the complexity of the ecosystem, and (4) a perspective of processes occurring in the drainage. Case-history studies such as that done at Carnation Creek meet these requirements and provide a strong basis for understanding the factors that control fish population sizes. Examination of similarities and differences of watershed processes among drainages where case histories have been obtained and drainages where habitat enhancement is being planned should be carried out to evaluate assumptions about habitat needs (Bisson 1989).

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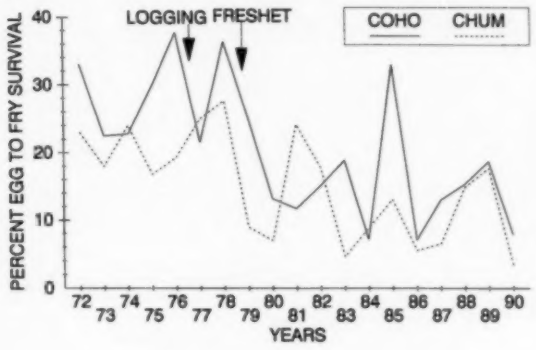
Fig. 8. Egg to fry survival for chum and coho salmon in Carnation Creek. Streamside logging was begun during 1976, which was followed by the first large freshet during 1978 (see Fig. 5).



Factors that limited Carnation Creek fish populations

Within the Carnation Creek drainage, the numbers of all four salmonid species were limited by different sets of factors. However, for each species the critical control period occurred during winter.

Chum salmon numbers were affected by two major watershed changes. First, erosion of stream banks in the lower 3 km and transport of the fine sediment downstream caused a decline in the quality and stability of chum spawning gravel (Scrivener and Brownlee 1989). The entombment of alevins and the scour and deposition of spawning gravel caused a 41% decline of egg to fry survival (Fig. 8) and a reduction of fry size following logging (Scrivener and Brownlee 1989). Second, following logging, stream temperatures increased during January–March, accelerating embryonic development and emergence of the fry (Holtby 1988). Fewer numbers of fry, earlier emigration to the ocean, and smaller size of fry caused fewer adults to return after logging (Scrivener 1991). Chum salmon survival at sea was also dependant on ocean conditions that had nothing to do with logging. Chum salmon returns to unlogged streams on the west coast of Vancouver Island declined with poor ocean conditions, but increased when conditions improved. Populations in streams within logged areas did not recover when ocean conditions improved (Scrivener 1991). Here, limiting factors shifted outside of the realm of any enhancement or restoration activity. Therefore, evaluation of habitat-improvement programs must include the ocean environment or managers might consider a project a failure when in fact poor ocean conditions affected the level of adult production.

The decline of spawning gravel quality and stability, and the increase of winter stream temperatures produced similar impacts on juvenile coho salmon, but they did not limit production in the population. Reduction of egg to fry survival (Fig. 8) and of fry size and acceleration of incubation and emergence timing were similar to those for chum salmon (Hartman and Scrivener 1990). Mean numbers of age 0+ coho during postlogging years were < 50% in late May and < 75% by the end of summer, of what they were in the prelogging period (Table 1). During postlogging years, however, growth rates increased when densities were reduced (Holtby and Scrivener 1989). This effect, plus the lengthening of the summer growing season, caused by earlier fry emergence, produced much larger juveniles by autumn (Holtby 1988). These large age 0+ coho had greater overwinter survivals (Table 1) and greater rates of smolt transformation at age 1+. Prior to logging, 50–75% of the smolts entering the ocean were age 1+ and the remainder were age 2+. Following logging, 95% of the smolts were age 1+ (Hartman and Scrivener 1990). Postlogging smolt numbers were similar to or greater than prelogging numbers but their annual variability increased threefold (Table 1).

Numbers of age 0+ coho declined progressively from spring to autumn, and the final number of smolts produced was set during the winter period when cover was critical (Table 1). Numbers of juvenile coho per unit of stream length was positively correlated with the volume of LWD that provided cover during both summer (Forward 1984) and periods of winter freshets (Tschaplinski and Hartman 1983). Choice of cover habitat increased with structural complexity of the habitat (McMahon and Hartman 1989). During winter, coho numbers in the main channel appeared limited by the volume of LWD with the correct structural complexity. During 1980–1989 in Carnation Creek, the number of fry at the end of September was greater than the winter carrying capacity of the stream in all years except two (Table 1). If incubation conditions were much poorer or if number of spawners were much smaller, control of smolt numbers would have shifted from winter rearing conditions for age 0+ coho to incubation conditions and egg to fry survival.

Coho production limits were also affected by the balance of use of off-channel and main-channel habitat and by the yearly changes of survival in the two habitat types. Age 0+ coho entered the floodplain habitat during September–November, and they exited from it during April and May (Fig. 3; Brown 1985). These areas were not significantly impacted by logging. However, survival and production were limited by winter and spring water levels (Brown 1985).

The few coho that remained in Carnation Creek for a second year did poorly in the post-logging environment. Summer growth rates and autumn size declined under the warmer temperature regime (Holtby and Scrivener 1989) and reduced food supply (Culp 1988). Physical habitat no longer appeared to limit their numbers, because almost all coho were now resident for only a single year (Table 1).

The altered age composition and size of coho smolts affected production stability and the numbers of returning adults. Smolts from two brood years stabilized smolt and adult production during prelogging years when large age 2+ smolts had high marine survivals (Holtby and Scrivener 1989). The large 2+ smolts were, however, rare during post-logging years so marine survivals declined and were more variable. The earlier emigration also caused reduced survivals in the ocean (Holtby 1988). If habitat improvement is carried out after logging in situations like Carnation Creek, it must be directed to the limiting stage in these sequence of changes. For coho production the critical stages occurred during winter.

Although we regard the amount and quality of winter habitat as being most important in determining coho smolt output, periods of drought or an elevated stream channel can reduce the amount of summer rearing space as a result of channel dewatering (Dolph et al. 1992). The channel has aggraded in

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Table 1. Numbers of coho fry at emergence and during stream surveys and fence counts in the lower 3070 m of Carnation Creek (1971–1982 data from Scrivener and Andersen 1984).

		Population estimation period			
	Population at emergence	Late May early June	Late July	Late September	Yearlings smots + resident
Prelogging period					
1970	—	—	16 004	14 129	2492
1971	157 400	37 030	29 188	11 842	3214
1972	50 320	33 556	15 578	9223	2509
1973	38 600	18 357	10 776	9071	2198
1974	37 420	17 580	14 589	12 460	1854
1975	44 770	14 605	14 092	11 482	2965
1976	58 800	46 662	19 173	12 327	2655
Mean	64 550	27 965	17 057	11 505	2555
SD	46 160	12 975	5905	1813	454
Logging period					
1977	23 460	15 767	14 338	10 602	5213
1978	39 825	26 148	23 120	10 927	4481
1979	30 400	26 347	19 702	13 227	5338
1980	48 625	—	25 756	20 953	5599
1981	17 200	6743	6995	6088	3152
1982	12 450	8648	8890	7337	3748
1983	27 650	17 304	11 720	10 184	3158
1984	6700	3209	4466	3423	1904
1985	15 000	12 589	12 303	6824	2850
1986	4150	2692	—	2916	2501
1987	14 606	6773	—	6584	2969
1988	8180	4242	—	5107	3753
1989	11 940	8780	—	7092	3217
Mean	20 014	11 603	14 143	8559	3682
SD	13 363	8243	7320	4784	1152

a few locations of Carnation Creek, isolating pools and inhibiting the movement of fish and aquatic insects especially during periods of low flows (Hartman and Scrivener 1990).

Impacts of logging on processes effecting cutthroat and steelhead trout were similar to that of coho salmon, but limiting factors were different. Trout spawned during the spring so when fry emerged early, the growing period was only lengthened by 1–2 wk. Their autumn size was significantly larger during post-logging years, but it did not increase overwinter survival or their transformation into smolts at age 1+ (Fig. 2). The size benefit gained during year 1 was lost during years 2 and 3 of stream residence (Hartman and Scrivener 1990). Cutthroat trout used the off-channel habitat both for spawning and winter rearing (age 0+, 1+, and 2+), so logging impacts on them were not as severe as for steelhead (Hartman and Scrivener 1990). Juvenile steelhead occupied only main-channel habitat. Coho, cutthroat, and steelhead had different patterns of distribution and use of the various parts of the watershed. Despite this, winter was the most critical period for production of each species.

Within Carnation Creek, the number of coho or trout smolts produced was controlled by complex interactions of both physical and biological processes, but factors that limited production were different for each species. Key elements that interacted to influence freshwater production were water temperature, condition of the incubation environment, amount of winter cover, and the balance of advantage and disadvantage of using off-channel habitat during any particular winter. Managers attempting to improve habitat must understand the relative importance and the interaction of these conditions before a project is begun.

Watershed restoration and habitat improvement: what does Carnation Creek tell us?

In the following section, we will discuss remedial strategies that could be used appropriately in watersheds like Carnation Creek. However, it must be recognized that headwater, hillslope, and channel conditions in this watershed are still changing rapidly at Carnation Creek.

Hillslope conditions and options

Conditions in the Carnation Creek drainage are still changing. Another 42% of the watershed was logged after 1987. This occurred in the steep headwater areas. More slides and debris torrents could occur in these areas, based on our experience during the first logging phase (Hartman and Scrivener 1990). To date, these areas have not been exposed to storm events with > 7-yr return periods (Fig. 5). Initial restoration projects should focus on road and slope stabilization. Attempts should be made to reduce further sediment supply by pulling back

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areas of unstable sidecast materials, diverting water off roads, removing culverts, reestablishing preexisting drainage channels and revegetating disturbed slopes. Removal of logging slash from torrent prone gullies may also be beneficial, if the remaining sediment and LWD is stable. It is, however, better to implement this kind of work immediately after logging, prior to the material being incorporated into the channel structure by processes of sediment deposition.

Riparian zone conditions

Conditions in the riparian zone have not stabilized at Carnation Creek (Scrivener and Tripp, in press). Areas of the alluvial floodplain that were logged to the stream bank 12 yr ago have not developed enough riparian vegetation to stabilize the banks. Restoration strategies here should assist with revegetation or wait for the volume of moving sediment to decline. Silvicultural practices to expedite the re-establishment of riparian shrubs and trees (including conifers and rapidly growing deciduous species) will eventually provide root-strengthened and erosion-resistant stream banks as well as a future supply of LWD. Measures to control localized bank erosion may be justified in some circumstances, particularly if this can be undertaken using bioengineering techniques (e.g., Schiechtl 1980). However, over the long term, the stream should be provided with a corridor within which it can freely migrate. Following restoration, few trees, if any, should be harvested from the riparian zone.

Habitat improvement within the channel

Once hillslope and riparian zone concerns have been addressed, it is appropriate to examine options for habitat improvement within the stream channel. However, it should be noted that a healthy or natural riparian zone would eventually produce a structurally diverse and productive stream channel, but it may require ≥ 90 yr after logging before these conditions are restored (Fig. 6). Therefore, work within the channel should expedite these natural processes and, as an interim measure, provide replacement habitat prior to its natural formation.

Keeley and Walters (1994) listed and evaluated a range of potential measures that might be used at Carnation Creek. LWD could be placed in sections of the channel that are devoid of it because of harvesting practices or subsequent removal by debris torrents, etc. These structures need to be well anchored and stable. They should provide areas of increased water depth and structural complexity for fish cover. However, they can also cause localized erosion of the stream banks either by redirecting stream flow or by causing sediment deposition, which redirects stream flow. Woody debris, placed in torrented streams on the Queen Charlotte Islands, provided habitat for young coho and steelhead with some success (D.B. Tripp, Tripp Biological Consultants, Nanaimo, B.C., personal communication). However, the LWD's anchors had to be buried 2 m below the streambed and their attached cables had to be 3.5 cm in diameter before the structures remained ≥ 5 yr. They captured floating logs, promoted sediment deposition, and attracted fish. If these structures had been placed in Carnation Creek, they might have exacerbated bank erosion and channel widening during 1984–1990. In some stream reaches, they would have been buried where large volumes of gravel were moving or abandoned when the channel relocated (Hartman and Scrivener 1990).

The complexity and location of LWD structures influenced the species composition of the stream community. Trout densities were less closely related to debris volume than were coho densities (Tschaplinski and Hartman 1983; Hartman and Brown 1987). Trout also tended to use plunge pools, caused by single, large, and partially buried logs, while coho salmon tended to use root wads and other structurally complex cover. In Kloyia Creek, coho preferred natural and artificial root wads that were near the banks, while trout preferred those that were away from shore (Shirvell 1990).

Placement of boulder clusters and log ramps (step dams) were listed as stream improvement techniques for small streams (Keeley and Walters 1994). In the Keogh River, boulder placement increased steelhead and coho densities (Ward and Slaney 1979). In the Chilliwack River, trout were more closely associated with boulder cover than were coho salmon (Hartman 1965). These methods appeared useful, but better design criteria are needed: specifically, involving studies to determine the rock size required for physical stability in different stream sizes, the rock densities at which stream sediment transport begins to alter significantly, and what kinds of stream environments are suited for enhancement with various types of structures (Lowe 1992; Rosgen and Fittante 1986). These structures might not be useful at this time in Carnation Creek, because they could compound problems caused by moving sediment, channel dewatering, and channel relocation.

Stream fertilization has merit as a stream habitat improvement technique. Its benefits have been shown in large streams like the Keogh River (Perrin et al. 1987; Johnston et al. 1990; Slaney et al. 1994). In Carnation Creek, low concentrations of natural phosphorus limited primary production (Stockner and Shortreed 1976). Production of periphyton and stream insects were increased by adding dissolved inorganic phosphorus to troughs at Carnation Creek (Mundie et al. 1991). Additions of nutrients might increase production of algae, insects, and fish. However, it should be demonstrated that production and food limit smolt output before substantial investment is made in enrichment programs. Mason (1976) increased the number of juvenile coho by artificial feeding. However, elevated numbers in autumn did not result in increased smolt production because winter habitat was limiting. Increased size of age 0+ coho, by autumn, improved overwinter survival in Carnation Creek. However, any gain achievable by enrichment may be limited by the amount of winter habitat. During winter, the relative importance of estuarine production and ephemeral satellite channels might become important for other watersheds (Cederholm et al. 1988).

Stabilizing stream banks with rip-rap may be regarded as a form of channel improvement. Studies on the Coldwater River (Lister et al. 1995) indicated that rip-rap can provide high quality juvenile chinook habitat if it is constructed of large rocks. However, rip-rap has not reduced bank erosion on agricultural land where valley bottom clearing and grazing have dramatically increased rates of channel shifting. Studies on the Deadman River, near Kamloops, B.C., indicated that prior to removal of riparian vegetation, the river channel was narrow, deep, laterally stable, and carried small amounts of bedload. Within areas of intensive grazing, the channel became wider, shallower, straighter, laterally mobile, and carried large quan-

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tities of coarse-textured sediments (Miles 1994). These studies suggested that attempts to control channel shifting by placement of rip-rap merely moved the area of active erosion downstream and further reduced fish access to a small number of remaining off-channel habitats. Here, a more appropriate strategy would have been to establish a corridor through which the river could freely shift, to provide fences to keep cattle from destroying riparian vegetation, and to replant the area stabilizing stream banks, providing shade and producing cover. Rip-rap placement would not improve channel conditions in Carnation Creek. However, providing a stream corridor, within which future logging was restricted or prohibited, would undoubtedly be beneficial from the perspective of both channel stability and fish habitat.

Off-channel habitat improvement

Streams with floodplain habitat hold some options for fish habitat expansion. Ponds and side channels might be built even if the main channel is very unstable. Overwinter survival and growth of coho and cutthroat were significantly higher in abandoned river oxbows and areas adjacent to wall-base channels[3] in tributaries to the Clearwater River, Washington, than they were in the main channel (Cederholm et al. 1988). It was an inexpensive technique that primarily benefitted coho salmon. In Carnation Creek, coho used sloughs and ephemeral tributaries on the floodplain, but cutthroat trout used only the ephemeral tributaries (Hartman and Scrivener 1990). Steelhead made little use of either habitats.

Off-channel construction in drainages like Carnation Creek would be less vulnerable than the main channel to the effects of elevated sediment loads, the deposition of pulses of sediment, and the erosion of stream banks. However, water on flood plains and terraces can be retained by a layer of fine sediments and decomposing vegetation that overlay the gravel (Brown 1987). Disruption of this layer could cause a loss of the perched water. Therefore, extreme caution is needed when doing construction in these habitats. Attempts at further enhancement in areas that already support fish might be limited to improving access. The optimum sites for creating new channels appear to be on fans, near the edge of the valley wall, or in areas where auxilliary water supply is available. In watersheds where coho salmon rear in the estuary, off-channel habitat might be built immediately upstream so that juvenile fish can move back into freshwater for the winter (Hartman and Scrivener 1990). Habitat would have to be constructed so that freshwater would flow through it during the winter. This type of project would enhance only coho salmon abundance, because most salmonids that use estuaries for summer rearing do not return to freshwater during autumn.

Expansion of estuary habitat might benefit spawning chum or pink salmon and rearing chinook salmon (Groot and Margolis 1991). Constructed areas of salt marsh (Adams and Whyte 1990), and zones of tidal shear and food production (Levings and Macdonald 1991) are used by juvenile chinook salmon.

If off-channel projects are envisioned for floodplain areas, either upstream or in locations close to an estuary, three requirements are necessary: (1) a water source to provide flushing and fish access; (2) sources of cover during cool winter temperatures; and (3) the project should not endanger existing water routing and availability.

Performance criteria for stream structures

Installation of the types of structures listed by Keeley and Walters (1994) has value, but we also need to understand and to predict their performance. We are not prescribing LWD piece size or density criteria; however, it may be inappropriate to attempt to reestablish LWD structures to prelogging densities in Carnation Creek. Sediment transport and peak flows were higher, and bank stability was lower, during the post-logging period. Because of this a high (prelogging) LWD density could lead to sediment deposition, bank erosion and structure instability, or relocation of the channel. A recent review of ~350 habitat-improvement structures indicated that channel processes affected their stability and performance (Fitch et al. 1994). Even in the comparatively benign streams of southwestern Alberta, structures were more successful in streams that were laterally and vertically stable, that carried small quantities of coarse textured bedload in comparison to total sediment load, and that had banks > 2.5 m high. Similar results were presented for streams in the Pacific Northwest (Frissell and Nawa 1992). Thus, instream structures may not perform well in the vertically and laterally mobile channels that commonly occur in logging impacted streams such as Carnation Creek.

Practical problems for fisheries enhancement projects are the lack of engineering criteria for structure design and the lack of hydrologic, hydraulic, and geomorphic data. This reflects both a lack of engineering and geomorphological advice during project design and a paucity of postconstruction assessment studies. Many manuals of stream enhancement structures exist but with the exception of Lowe (1992), none provided dimensions, rock sizes, or other engineering specifications. Similarly, more analyses like those of Rosgen and Fittante (1986) are needed to determine what structures are suited or unsuited for particular types of stream channels.

Even with better design guidelines, it may not be practical to build instream structures that are sufficiently robust to function effectively in high-energy streams. For example, an analysis of boulder placements in southwestern Alberta streams indicated that they had to be ≥ 23 times larger than the streambed mean particle size before they would remain in place (Fitch et al. 1994). If these results are verified, it may be physically impossible to move boulders of sufficient size to be stable in many west coast streams. Flume studies have indicated that single roughness elements cause a maximum flow resistance when they cover 10% of the channel bed, but they have relatively little effect at ~1% (Koloseus and Davidian 1966). This implies that boulder densities should be quite low, ~1% of the bed surface, if significant changes in channel resistance and sediment deposition patterns with very high sediment loads are to be avoided for streams. Studies on the Coquihalla River, a high-energy stream in southwestern British Columbia, also indicate that a 20-yr return period flood can substantially entrain or even bury very large boulder groups (Miles and Associates Ltd. 1994). Thus, periodic monitoring

[3] Wall-base channels are floodplain channels that collect and transport runoff from the base of valley walls to permanent streams. They often develop along abandoned meander scars and swales.

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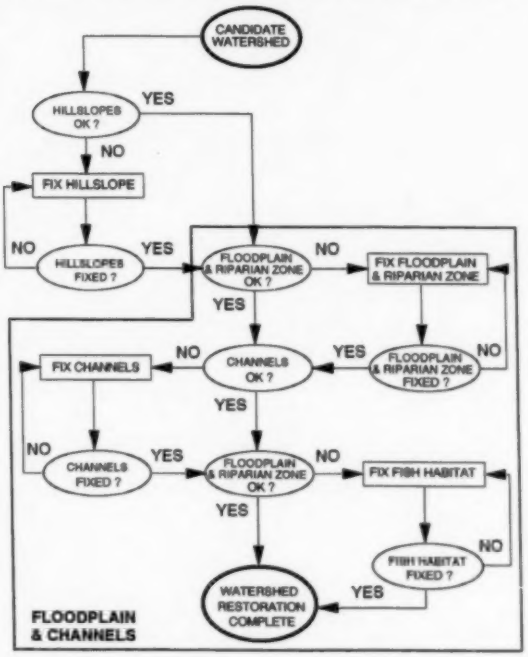
Fig. 9. Decision making hierarchy proposed, by D. Hogan, for use in the Watershed Restoration Program which is being implemented in British Columbia (Redrawn from Moore 1994).



and repairs may be required to maintain instream structure performance.

The corridor required as a channel-meander zone should be determined by characteristics of the river and not by artificial rules, such as a 10–30 m wide leavestrip. Two approachs to this problem can be made using typical relationships of hydraulic geometry. The radius of curvature for a stream meander is typically 2.3 times the bankfull width of the channel. Thus, the corridor that would contain two opposing bends would be ~6 channel widths (Newbury 1994). Second, pool-riffle or meander bend sequences tend to reoccur every five to seven channel widths. Therefore, if one riffle-pool sequence was to form across the valley, a width of ≥ 6 times the bankfull channel would be required. A corridor as much as 10–14 channel widths might, however, be necessary for unstable streams to provide enough space for vegetation to form erosion-resistant banks.

Planning, building, and evaluating projects

Watershed restoration and stream improvement projects require steps of proper planning, construction, and evaluation. Programs with all three components are seen infrequently.

Planning

Planning of large-scale projects requires institutional arrangements that are seldom made. Project teams should be interdisciplinary and the individuals should work closely with some type of public advisory group. Large-scale watershed projects must include fish biologists, plant ecologists, hydrologists, geomorphologists, foresters, wildlife biologists, and economists. Small-scale habitat improvement projects involving placement of structures in stream should be developed with geomorphological and engineering advice.

Projects planned following logging require a systematic analysis to establish where effort should be focussed. The Watershed Restoration Program, under development in British Columbia, uses a hierarchical implementation sequence that attempts to examine and then restore hill slopes, riparian zones, channels, and fish habitat in this order (Fig. 9). Thus, a system is established that avoids channel work in unstable streams like Carnation Creek, until such times as hill slopes and riparian areas have been stabilized. The following kinds of information are necessary for a hierarchical analysis: (1) the potential sources of slides, sediment, and debris; (2) the nature of upslope processes; (3) conditions in steep gully tributaries; (4) the potential for transmission of impacts to downstream locations; and (5) processes that are occurring in the lower reaches of the stream channel.

If the analysis and planning process leads to a program of stream habitat improvement, to increase abundance of fish by replacing lost habitat or by improving habitat, two matters must be understood. First, the appropriate species must be selected for enhancement. Second, the life-history stage where primary limitation occurs, and the processes by which it occurs must be understood. Although it seems obvious that such assessments should be made, it is not always done. Frequently decisions about habitat needs are based on judgement or biological intuition. In the mitigation program for the Oldman River Dam Project in Alberta, the priority assigned to species, the decision about the target life stage, and the type of habitat improvement measures required (Dominion Ecological Consulting Ltd. and J.N. Mackenzie Engineering Ltd. 1988) were based on judgement and assumptions. The survey work was extensive, but there was no experimental analysis of population limitation even though this was a very large-scale program (FEARO 1991). A major program of remedial measures compensating for flow reductions in the Nechako River focussed on the provision of cover for juvenile chinook salmon. The decision to enhance this life stage of chinook in such a manner was based on judgement and intuition about needs and not on research information that identified the juvenile rearing stage as the one that limited population production (Anonymous 1987).

For small stream improvement projects in British Columbia, the life stages of fish species and the limiting factors that are targeted for enhancement are usually chosen from management experience and judgement. This is understandable because it may be impractical to do population analyses for limiting factors during small projects. However, the use of judgement or intuition are inappropriate where substantial sums of money are being spent.

Before any restoration project is approved for action, the timing of evaluations, their criteria, and the reporting sequence should be developed. Conditions for project abandonment should also be agreed upon. Small-scale projects should not be allowed to "fall between the cracks" because of staff changes. The planning process should be guided by policy that determines how intense efforts should be to increase fish numbers. In British Columbia, emphasis is shifting toward ecosystem management and concern about maintaining biodiversity. Historically, biologists and members of the public have expressed

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concern about a single-use philosophy that they perceived in the forest industry. The single use of streams as fish production areas may also not be appropriate; therefore, it may be inadvisable to construct large numbers of instream structures on specific river reaches, as was done in southern Alberta as part of the Oldman River Dam project.

Construction

Construction for watershed restoration projects is different than for stream habitat improvement and may involve more risk to personnel. Work on the hill slopes requires costly machine time and high skill level for activities such as road resloping and debris removal from steep gullies. There may be risks to workers when steep and unstable gullies are cleared, or when machines are placed on old road grades. Operational limitations should be understood before projects are designed.

Sound construction and appropriate design are both necessary components for stream channel improvement. Many techniques are described, including streambank stabilization, riparian planting, streambank fencing, gravel placement, gravel cleaning, construction of cover, fertilization, and off-channel development (Adams and Whyte 1990). The features that affect the biological merits of using such structures or techniques have been considered by Reeves et al. (1991). Keeley and Walters (1994) listed techniques for stream and riparian zone restoration and classified those most useful for small streams. Both evaluations assumed that the construction is sound. However, these assumptions are not always met. Forty-four percent of 100 structures built in British Columbia, and evaluated by Hartman and Miles (1995), were of limited durability or failed. It was not possible to separate the roles of design and construction in these failures. However, some boulder placement projects had used rocks that were too small. Other installations were successful because workers made the special effort of installing large boulders on carefully constructed pads of smaller ones. Some log placement projects failed because the cables used were too small. In the Mount Hood National Forest, structures that were installed with heavy machinery were more durable than those constructed by hand. After 15- to 20-yr floods, 90% of heavy equipment structures and 60% of the hand-built structures were still functional (Higgins and Forsgren 1987).

Preparation for construction must at least include (1) consideration of risk to workers, (2) determination that design materials are available and can be used, and (3) consideration of the method of installing structures that will provide the highest physical durability.

Evaluation

Evaluation should be done on all projects to determine the following.

Physical performance

(1) If roads were resloped and deactivated, if sediment and debris were removed from gullies, or if eroding slopes were reseeded in watershed restoration, did these measures succeed physically?

(2) If stream structures were built for habitat improvement, were they durable and did they remain in the physical context that was intended?

(3) If the structures or restoration were not durable, how much maintenance was required?

Biological performance

(1) Did the works accomplish what was intended?

(2) Did structures increase population production or simply change fish distribution?

(3) Did the structures cause loss of productivity of one species, while increasing that of another?

(4) What was the population increase if it occurred?

Economic benefits

(1) What was the value of the production increment over natural background levels?

(2) What was the amortized cost of construction?

(3) What was the cost of maintenance?

The economic evaluation must be of adequate intensity and duration to be valid. Projects targetting natural populations of salmonids probably require 6–7 yrs to produce population changes (Hunt 1976), so evaluation must extend over a period that detects such change. Evaluation is very weak, or absent, during most projects (Lowe 1992; Frissell and Nawa 1992; Miles 1994; Fitch et al. 1994). A small sample of mitigation projects was reviewed for the Oldman River Dam Project. Only 8 of 41 projects were evaluated for > 4 yrs (FEARO 1991). In British Columbia, only 2–5% of the small fisheries projects were reported on after 7 yrs.

The record of progress of projects must be available to the public. Sound evaluation is needed to provide this information. Funding and the continuation of programs depends upon public satisfaction and trust. People may accept a degree of openly reported failure. However, they may not continue to accept information that is vague or suggests incompetence.

Conclusions

The Carnation Creek studies provided some understanding of the types of processes that managers should be aware of or appreciate before entering into projects of watershed restoration or stream habitat improvement:

(1) There is a high level of complexity in natural ecosystems. We can not always judge correctly what the critical factors or times are in the life of populations of fish.

(2) Physical conditions caused by forestry activities change at different rates over time. There may also be sets of physical processes occurring that overlap and compound their effects.

(3) Forestry impacts have different effects on different species and life stages of fish.

Experience with a number of habitat improvement projects and consideration of processes in Carnation Creek indicate that (1) the planning and development phase of projects is often weak; (2) experimental design for evaluation of projects is weak or absent (even the Carnation Creek Project did not

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have a separate control watershed of similar size); (3) a hierarchical approach to planning watershed, riparian, and stream-channel improvement is a valuable and essential foundation.

Much of this paper has focussed on problems of doing stream restoration and habitat improvement. We do not wish to discourage this work. However, we believe that too much of it is done with little or no use of science. Good science and well-structured management programs must merge in any fish habitat improvement project. We must understand basic watershed ecology and use sound practical judgement to restore habitat.

Fisheries biologists must begin considering limits to stream improvement work. Many structures are unnatural and offend other stream users and even some people who fish. A broad sector of stream users must eventually decide the scale, type, and location of stream-improvement projects.

Finally, it may not always be possible to repair the damage caused by decades of irresponsible land use. We must understand that we may be able to destroy things more readily than we can repair them. Restoration is a poor substitute for habitat protection.

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Integrating biological realism into habitat restoration and conservation strategies for small streams

Charles F. Rabeni and Scott P. Sowa

Abstract: Successful habitat conservation or restoration must be biologically based, which requires an understanding of habitat variables most influencing fish; the relative influence of each habitat variable and the spatial scale over which each operates. Determining necessary habitat conditions requires examination from several perspectives, including observation of individual fish during all seasons and population analysis over a range of spatial scales. There is a definite spatial hierarchy of influences that must be addressed to separate those habitat conditions responsible for presence and abundance from those habitat conditions responsible for within-stream distribution. A case study of habitat factors influencing smallmouth bass (*Micropterus dolomieu*) in Missouri streams indicates that examination at the smallest spatial scales allows one to determine the influence of habitat conditions (depths, velocities, cover factors) relating mainly to the fish's distribution in a stream reach. Evaluation of populations at the stream-system level allows an understanding of how individual fish preferences relate to amounts of habitat as determined by geomorphic and fluvial dynamic forces and how this influences standing stocks throughout a stream system. Evaluation at the ecoregion level shows the overriding influence of physiographic variables on both the presence and abundance of fish across stream systems, as well as the importance of land use.

Résumé : La conservation ou la restauration de l'habitat se doivent, pour réussir, de reposer sur des fondements biologiques. Cela suppose de connaître les variables de l'habitat qui influent le plus sur le poisson de même que l'incidence relative et l'échelle d'action spatiale de chacune de ces variables. La détermination des conditions de l'habitat nécessaires exige de réaliser un examen sous des angles divers, notamment l'observation de poissons donnés pendant toutes les saisons et une analyse de population portant sur une gamme d'échelles spatiales. Il existe une hiérarchie spatiale nette des influences qui doit être évaluée afin de distinguer entre les conditions de l'habitat régissant la présence et l'abondance et celles régissant la répartition au sein du cours d'eau. Une étude de cas des facteurs de l'habitat influant sur l'achigan à petite bouche de cours d'eau du Missouri montre qu'un examen aux plus petites échelles spatiales permet de déterminer l'influence des conditions de l'habitat (profondeur, vitesse du courant, couverture) qui ont surtout trait à la distribution du poisson dans un segment du cours d'eau. L'évaluation des populations à l'échelle des ramifications du cours d'eau permet de comprendre la relation entre les préférences de poissons donnés et le volume d'habitat, lui-même déterminé par les forces géomorphiques et dynamiques fluviales, et comment elle influe sur les stocks présents dans le bassin du cours d'eau. L'évaluation au niveau de l'écorégion montre l'influence prépondérante des variables physiographiques sur la présence et l'abondance du poisson dans les bassins de cours d'eau, de même que l'importance de l'utilisation des terres.
[Traduit par la Rédaction]

Introduction

Understanding the linkage between habitat and the well being of fish populations is an obvious first step in any efficient, effective conservation or restoration strategy. Yet, surprisingly little empirical evidence of this sort exists for coolwater or warmwater streams in midcontinental North America. Efforts to "improve the quality of stream fishing" usually focus on altering physical habitat, as if physical habitat were a magic wand controlling fish abundance and distribution. The theoretical basis for such optimism is well founded; such as in Southwood's (1977) habitat templet framework, where many ecological attributes of organisms are viewed as related to the spatial and temporal availability and predictability of habitats. Yet, fish population responses to habitat alterations are seldom predictable, and the efficacy of "habitat improvement" in warmwater streams is rarely demonstrated (Lyons and Courtney 1990).

While habitat improvement strategies need to be based upon ecologically sound principles where relations among habitat elements and fish populations have been demonstrated, they must also be carried out with an understanding of the potential capacity (sensu Warren et al. 1979) of the system to support fish. The potential capacity of most midcontinental North American streams to support fish has substantially diminished since the arrival of European settlers. In Ohio, for example, there were reports around 1800 of "huge populations of the larger and better food and game fishes: pikes, walleye, catfishes, suckers, drum, sturgeon and black basses" (Trautman 1981). However, within 50 years, extensive

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draining and filling of marshes had irrevocably altered headwater conditions such that many permanent springs and brooks became intermittent, and the shallow, ephemeral wetlands required for reproduction of many species were lost. By 1900 increasing agricultural activity and within-channel and riparian modifications created numerous clay-bottom streams; siltation became the most important pollutant affecting fish fauna. Thus, the major damage to warmwater streams probably occurred within the first 50 or so years of European settlement and the situation has been generally exacerbated since then. Most stream degradation is ecologically undocumented, and we now have the problem of determining after the fact system potential and the important factors limiting such potential.

The conceptual framework

Stream habitat is defined by Milner et al. (1985) as "the local physico-chemical and biological features of a site that constitute the daily environment of fish." Of importance to management is that while fish respond to local conditions, some of those conditions originate far from the stream. Some elements of the habitat are a reflection of broader scale influences: the "pervasive nature of the environment" (Ryder and Kerr 1989) or "watershed influences" (Rabeni 1992). These factors provide the environmental setting and, in small midcontinental streams, consist of water temperature, nutrients, dissolved oxygen, and flow regime. One should be less concerned with the local structured habitat as a limiting factor until the more fundamental properties of the environment have been examined, because some of these broader based influences determine both the relative livability of a stream for a population and its potential capacity. The importance of various habitat factors influencing fish distribution and abundance may depend upon the scale at which they are examined (Fausch et al. 1994). Therefore, restoration strategies incorporating a multiscale approach will be more effective in identifying true mechanisms regulating populations.

A hierarchical framework for classifying streams was developed by Frissell et al. (1986), in which smaller scale systems develop within constraints set by the larger scale systems of which they are part. This perspective allows us to view some local stream influences as originating at the largest spatial scales, affecting entire stream systems, and their components: stream segments, reaches, pool-riffles, and microhabitats. Because the hierarchy of habitats can be considered spatially nested, such that an influence at a particular scale can affect all smaller scales, management activities (e.g., remedial measures improving degradations) will be most successful if they attack the highest level where the influence occurs. Management activities at a local, say pool-riffle, scale will likely be inappropriate if the hydrology at a stream-system level has been severely altered. The factors controlling stream potential capacity and general livability usually emerge from the largest spatial scales: stream systems or even ecoregions. Factors pertaining to physical habitat operate at the smallest scales: pool-riffle or microhabitat. Because the scales are nested, livability factors can override anything done at the pool-riffle level, but the opposite is not true. Thus, conservation or restoration strategies that are biologically realistic involve understanding the factors responsible for influencing fish, the source and spatial scale involved with the controlling variables, and the relative influence of each variable on the stream's potential to support fish.

Determining fish-habitat relations

Determining those habitat conditions required for a population of stream fish is often problematical. Often, conditions thought to be very important or even essential may have readily available substitutes (e.g., rootwads versus deep water as cover for smallmouth bass (*Micropterus dolomieu*)). Sometimes habitat elements unused by fish are important as food-source areas or as barriers to predators or competitors. Some habitat conditions, such as an unexpected spate, may be disastrous to a population in the short term if it comes right after spawning, but it may also be essential in the long term for scouring holes and undercut banks and otherwise maintaining a diverse physical environment. Further complications arise when habitat conditions needed by fish change temporally by diel and seasonal periodicity and by life stage. Nevertheless, a prerequisite to habitat improvement should be understanding the habitat elements required by fish.

We believe the approach used to obtain fish habitat information determines the usefulness of the results to fisheries management. Generally speaking, two approaches to fish habitat analysis in streams have been taken: investigating behavioral associations of individuals at a small spatial scale and determining associations of habitat elements with populations at a larger, and perhaps coarser, spatial scale. Each approach has advantages as well as drawbacks and we believe a discussion of the merits of each approach would be useful.

Behavioral associations with habitat

Fish-habitat associations at the pool-riffle or microhabitat level are determined by detecting (visually or by telemetry) or collecting (usually by electrofishing or seining) fish and measuring habitat variables at that spot (Rinne 1985; Winter and Ross 1981). Either the percentage of total time individual fish occur in a habitat (Cunjak and Green 1983) or the percentage of total fish in a habitat in any particular time (Bart 1989) are determined. The resulting data are habitat "use", and the use of a particular variable is compared relative to others.

Biologists often assume that a habitat element "used" out of proportion to its "availability" is either "preferred" or "avoided" (Baldridge and Amos 1981), and refinements were made to quantify this relationship (Jones et al. 1984; Kinzie 1988). This "preference" concept gained wide acceptance since Ivlev (1961) developed his electivity index for quantifying fish feeding relations and has been improved upon either using Ivlev's general approach (e.g., Strauss 1979; Jacobs 1974) or by modifications: chi-square analysis (Neu et al. 1974; Byers et al. 1984) or a ranking method (Johnson 1980). Other studies have compared the methods or examined their statistical properties (Thomas and Taylor 1990; Alldredge and Ratti 1986), which while adding some statistical elegance, have perhaps given the concept unwarranted legitimacy, because the biological basis for this concept remains suspect.

An implicit assumption often made when use or preference data are applied to management is that a behavioral response

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of individual fish (i.e., associating with a particular habitat element) has some relevance to the population variables managers are really interested in, such as density, growth, mortality, or reproduction. There is very little basis in fact that either habitat use or preference equates with habitat importance or that habitat amounts relate to fish amounts.

A fish has to be somewhere in a stream, and there may be numerous locations where it would do fairly well. Although it has been demonstrated that trout position themselves to maximize energy input and minimize energy expenditure (Fausch 1984), having to occupy less than optimum locations does not necessarily mean the population is in peril. Most fish in coolwater or warmwater streams use available habitat in a dynamic manner. Most species are not microhabitat specialists, but occupy rather broad ranges of habitat conditions (Moyle and Baltz 1985; Bart 1989) modified by several factors, e.g., competition or predation (Gorman 1988), that are rarely taken into account in this type of analysis.

We view use data as necessary but not usually sufficient to base management strategies. If a fish associates with a habitat element much of the time, then that habitat element is probably important, but perhaps not important enough to be a limiting factor. If a fish never associates with a habitat element, it may be unimportant, it may be detrimental if used, or it may be essential by providing food or eliminating predators or competitors.

Use or preference analysis is usually applied on some of the smallest spatial scales a biologist considers: local depth, current velocity, substrate condition, and cover. While behavioral associations with microhabitat features are no doubt important, biologists cannot ignore that fish distribution and abundance are influenced by larger scale factors, such as basin-level variables: geology (Fraley and Graham 1981), topography, area, elevation, stream size, gradient (Kozel et al. 1989, Chisholm and Hubert 1986), temperature (Swales et al. 1986), and discharge variables dealing with peak flows, minimum flows, and flow variation (Poff and Ward 1989). Often, only when basin-level habitat variables are appropriate (e.g., flow or sedimentation) for a fish population will microhabitat variables (current, velocity, substrate) be important and worthy of expending resources.

Population associations with habitat

The alternative to the microhabitat-based behavioral study for learning about fish-habitat relations is the approach relating habitat elements to some aspect of fish populations, often under the rubric of "Habitat Evaluation Models" (see Rabeni 1992 for a review). A general feature of these models is an equation relating some independent habitat variables that the biologist measures, to determine the value of a single output (dependent variable) about habitat quality or a fish characteristic. The models with habitat quality as an output variable (many habitat quality indices) have no direct relation to fish, other than the implied one that as habitat quality increases, so do certain desirable attributes of the fish population of interest. Of more relevance to our theme of biological realism are models relating fish characteristics (sometimes presence or absence, sometimes density or biomass) with habitat features.

Methods that predict density or biomass as output variables are usually empirically derived where habitat variables and fish abundance are measured at several different sites and then related by statistical techniques such as regression analysis. (Fausch et al. (1988) provide an excellent review of nearly 100 such models.) Usually a number of habitat variables are tried until the statistically best ones are found. This approach has appeal because it identifies habitat variables that account for much of the variation in fish characteristics, makes fewer initial assumptions about the importance of particular variables, and the models can be (but rarely are) tested.

These models can be misused because conclusions from highly significant correlations can be mistaken as causal and, therefore, predictive of the outcomes of management efforts. While some models have been validated, few have been experimentally verified. A notable exception is the work by Thorn (1988, 1989) who developed regression models relating brown trout (*Salmo trutta*) to habitat characteristics, primarily overhead cover and depths, in some Minnesota streams. The models were then used, a priori, to predict changes in standing crop before habitat improvements were made. A postimprovement evaluation showed that the change in the trout population was remarkably close to that predicted. Only when models have gone through this type of rigorous testing can they be used with confidence as management tools.

Of particular concern is that many models lack geographical transferability (Shirvell 1989). For example, Binns and Eiserman's (1979), trout-habitat model developed for Wyoming streams was not suitable for Ontario (Bowlby and Roff 1986) or Montana (White et al. 1983). Nevertheless, the approach has merit when models are used at the scale and in the area where they were developed, and they should not be expected to perform well in other situations. Most success is shown when investigators choose a well-defined area, be it site, watershed, or ecoregion, that is fairly homogeneous in basic physiographic characteristics, and develop a model from the full complement of variable continuums available throughout that location or area. Models may then be used successfully on an ecoregion scale to predict habitat conditions necessary for a species to be present (e.g., smallmouth bass in Wisconsin streams (Lyons 1991)), in more localized geographic areas for delineating critical habitat for endangered species (e.g., gila trout (*Oncorhynchus gilae*) in Arizona; Rinne 1978), or determining factors with the potential for enhancement of sport fish within a single stream system (e.g., smallmouth bass in Missouri (McClendon and Rabeni 1987)).

Even so, the approach is purely inductive, and ancillary evidence is needed to infer causality. While such studies may be useful for predicting fish characteristics based on habitat characteristics, it is not the same as knowing that habitat modifications will produce a particular change in standing crop or biomass.

Smallmouth bass case history

Based on the preceding discussion, we present an evaluation of the relations of smallmouth bass to environmental or habitat conditions in Missouri streams taken at three spatial scales: the ecoregion (defined by Omernik 1987), the stream system, and the stream reach (defined by Frissell et al. 1986; Fig. 1). We will illustrate how taking a multiple approach (asking different questions at different scales) helps discern essential habitat elements that could be a focus for management efforts.

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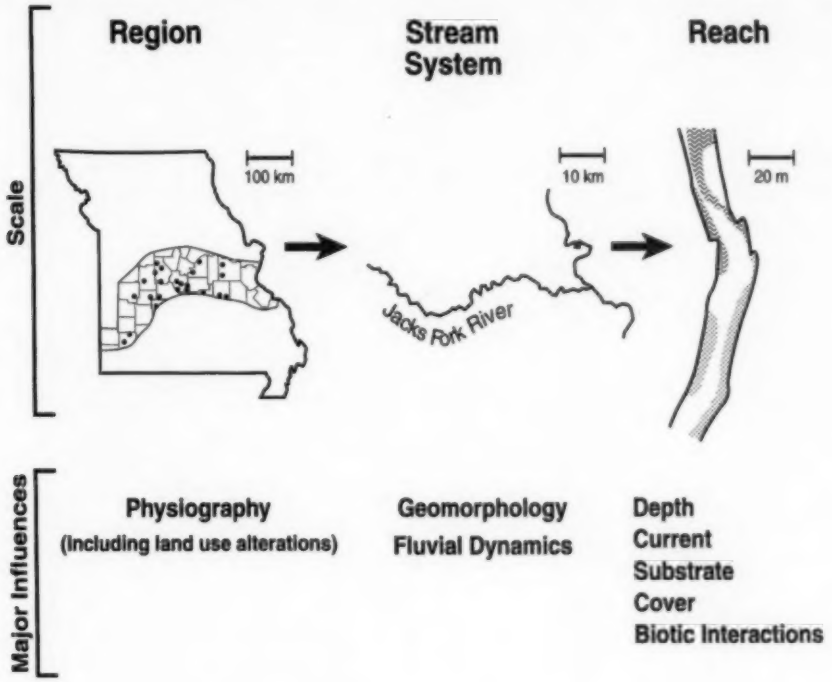
Fig. 1. Organization of the three spatial scales studied, indicating the major influences on distribution or abundance smallmouth bass at each scale.



Microhabitat (pool-riffle scale) analysis

An evaluation was made of how fish used their local habitat in terms of depths, current velocities, substrates, and cover attributes. Daytime habitat use by fish in summer was documented using underwater observations (Figs. 2*a* and 2*b*; Probst et al. 1984). Over 90% of the individuals were found to be positioned within 1 m of some type of structure, e.g., log, rootwad, or boulder. Cover was not important in interspecific segregation from other centrarchids. Water depth and current velocity were important as elements of intraspecific segregation. Substrate use appeared to be dependent on cover use, and results were inconclusive. A subsequent telemetry study (Todd and Rabeni 1989) substantiated observational studies and added information on fish habitat associations in darkness and in winter, when fish used boulders to a great extent (Fig. 2*c*). Both studies showed how smallmouth bass avoided shallow areas and existed almost exclusively in current velocities < 0.2 m/s.

Results of these studies emphasizing individual fish delineated how the fish used their immediate environment, how use changed both on a diel and seasonal basis as fish grew, and how habitat use was apparently influenced by size and other species. As interesting as this information might be, it has limited usefulness to management by itself. This approach cannot tell much about population requirements or how any habitat manipulation could improve a fishery. It tells us nothing about system potential but perhaps something about very local habitat potential, which is often extremely useful when used with other information.

Mesohabitat (stream system scale) analysis

Regression models relating habitat to density and biomass, developed from populations in 20 different stream sections of the same river system (McClendon and Rabeni 1987), seemingly contradicted conclusions from the behavioral studies (Table 1). The population-level study indicated that aspects of depth, current velocity, and woody structure were not correlated well with standing stock of smallmouth bass. What the regression models did show was that the amount of boulders had a positive relation to both density and biomass. No cause and effect could be inferred, but boulders, as our telemetry studies indicated, were used the majority of the time by smallmouth bass during the winter months. Perhaps boulders are an essential habitat or a limiting factor for smallmouth bass in these streams because of some important, yet still unclear, function during cold-water periods. In many Ozark streams, substrate particles > 200 mm are a unique component of a hydrologic habitat unit termed Bluff Pool (Rabeni and Jacobson 1993). A typical bluff pool has a steep outer bank adjacent to bedrock, whereas the inside bank and the upstream and downstream boundaries are gentle slopes underlain by gravel and containing extensive concentrations of boulder-sized substrate particles.

The geomorphic forces that shape a particular reach-scale habitat, comprising a mosaic of hydraulic habitat units, are different in different parts of the basin. In the upstream areas, stream valleys are incised into bedrock and flow in narrow valleys bordered by steep bedrock bluffs. Valley widths are

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Table 1. Regression equations relating smallmouth bass density (no.·ha^{-1}) and biomass (kg·ha^{-1}) to habitat variables at the stream system (McClendon and Rabeni 1987) and ecoregion (Sowa and Rabeni 1995) levels.

	F	R^2
Jacks Fork River		
Density = 43.86 + 574.44(area of boulder) + 5.79(area of undercut bank)	5.64**	0.62
Biomass = 12.32 + 1.31(area of undercut bank) + 74.34(area of boulder)	4.40*	0.56
Ozark Border region		
Density = 345.00 – 9.00(maximum summer temperature) – 90.00(percent pool area)	15.08**	0.54
Biomass = 51.42 – 1.22(maximum summer temperature) – 16.60(percent pool area)	16.53**	0.54

* Significant at $\alpha = 0.10$.
** Significant at $\alpha = 0.05$

Fig. 2. Relations of smallmouth bass to habitat elements at the microhabitat scale indicating the influence of (A) water depth, (B) current velocities on different sized fish, and (C) preferences of adult fish for particular habitat elements in two seasons. Data were reanalyzed from Probst et al. (1984) and Todd and Rabeni (1989).

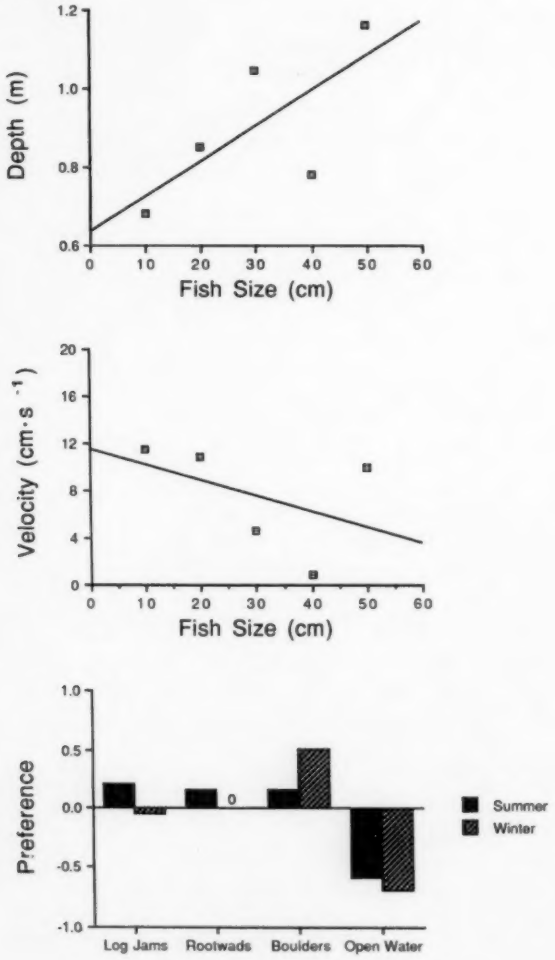
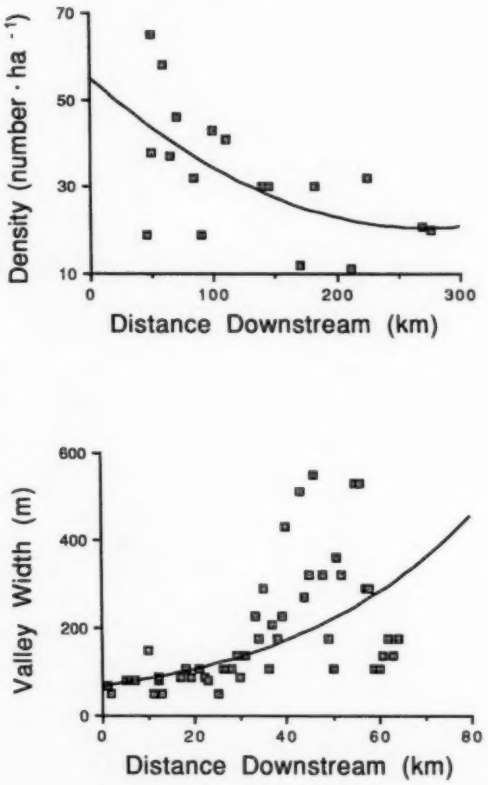


Fig. 3. Longitudinal changes in densities of smallmouth bass as related to changes in stream valley width (Rabeni and Jacobson 1993).



60–90 m and sinuosity is low, typically 1.05. Stream channels are rectilinear with long straight reaches along valley walls alternating with sharp bends where the channel crosses the valley to the other valley wall. Along bedrock bluffs and at junctions with steep tributaries, coarse cobbles and boulders dominate the bed material. At bends, bed and bank materials are typically coarse gravel to sand.

Downstream, narrow valley sections tend to be replaced by wider valley bottoms mantled with alluvium. Valley gradients

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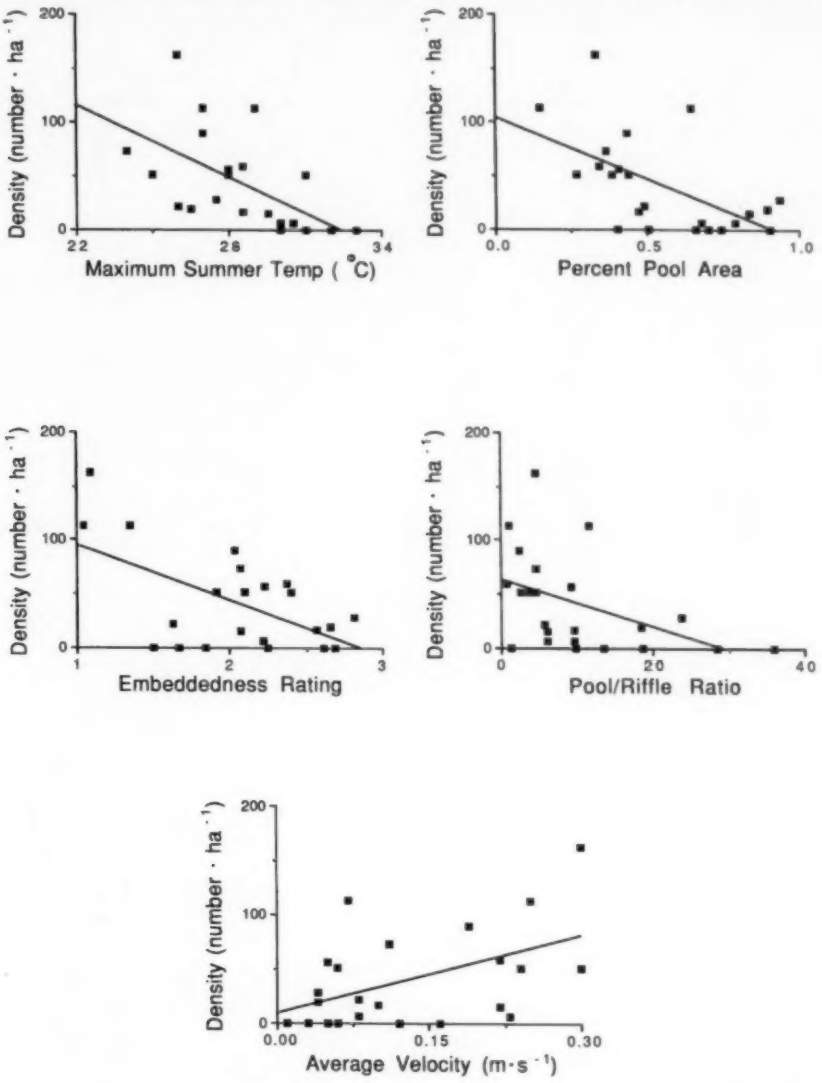
Fig. 4. Region-wide relations of smallmouth bass densities to important habitat characteristics (adapted from Sowa and Rabeni 1995).



are slightly less than upstream and valley widths are 400–650 m; sinuosity increases slightly to 1.09. As valleys widen, bedrock bluffs become a smaller proportion of its length and the channel is increasingly bordered by alluvial materials. Wider valley sections have a greater proportion of gravel and sand in the bed material, and a smaller proportion of cobbles and boulders.

These physical data indicate a systematic habitat variation related to geomorphic processes at the basin (stream-system) level. Populations of smallmouth bass are greatest in our upstream reaches (Fig. 3), and there is a notable negative relation between fish density and valley width, although many other factors are likely involved. Habitat types most used by fishes are also proportionally more abundant in upstream areas. For example, the ratio of bluff pool (which possesses not only boulders but more of the preferred current velocities and depths), to fine run habitat (small substrate, shallow), is greater than 10:1 near km 10 in Fig. 3 and is reduced to less than 1:1 near km 50. This suggests that not only do fish use, perhaps prefer, certain habitat types (indicated from microhabitat analysis), but there is also a relation between fish preference and fish abundance. This analysis shows a longitudinal change in reach potential within a system and how this potential could be predicted by simple habitat variables controlled by geomorphic processes and fluvial dynamics.

Macrohabitat (regional-scale) analysis

We examined habitat conditions associated with the distribution and abundance of smallmouth bass throughout a physiog-

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raphic division of Missouri known as the Ozark Border region (Fig. 1; Sowa and Rabeni 1995) to identify causes of declines in numbers. Quantitative data for both fish and habitat were collected at 23 sites from 19 different streams. Five of the 22 habitat variables measured revealed significant associations ($r \geq 0.30$) with smallmouth bass density (Fig. 4) and biomass, which in order of importance were maximum temperature, percent pool area, substrate embeddedness, pool to riffle ratio, and mean water velocity.

We developed multiple-regression models to predict the density and biomass of smallmouth bass based upon habitat features (Table 1). Of the five initially important variables, only two (maximum summer temperature and percent pool area) significantly contributed to the final models. Generally, the significant variables related to broad-scale features of the physiographic setting. We suspect these variables were important in the models because historic temperature extremes increased and pool-riffle morphometry changed to more uniform run-pool conditions because of widespread logging, grazing, row-crop agriculture, and road construction activities in the region (Bauman 1945). Thus, not only were we able to identify habitat conditions associated with a stream's potential to support smallmouth bass throughout a region, we were also able to generate quantitative equations to predict this potential with relatively good accuracy, using only two habitat variables.

In no instance in this regional study was cover associated with the abundance of smallmouth bass across streams, a contradiction to the conclusion reached from the microhabitat studies. However, when examining adjacent 250-m reaches within each stream, in 19 of 23 cases combined smallmouth and largemouth bass density was greater in those sections with the most total cover (paired t-test, $P < 0.05$). This suggests cover is more important in determining the distribution of smallmouth bass within streams rather than the abundance or presence-absence of smallmouth bass among streams.

Conclusions

We found a hierarchical approach to be useful in examining fish-habitat relations. Examination at one spatial scale assisted us in assessing fish potential at the next lower level. From the ecoregional analysis we found some general pervasive conditions of physiography, as modified by land use, which determined capacity among stream systems. The mesoscale (stream-system) analysis exposed the importance of fluvial dynamics within a stream system in setting stream reach capacity. The microscale (pool-riffle) analysis pinpointed particular habitat elements at the local spatial scale that, all other things being equal, probably contribute to abundance and explain distributions. No one analysis would allow us such a comprehensive view.

The collective information gained from this hierarchical approach aids determining where conservation and restoration efforts might be most effectively placed. We believe that restoring smallmouth bass populations in Missouri will require more than just local habitat manipulations. Efforts must focus on minimizing solar and fine sediment inputs and restoring proper pool-riffle morphometry. Additionally, we must conserve and generate further understanding of the importance of the "bluff pools." Providing additional cover to enhance smallmouth bass populations should only be attempted when the system approaches the "known" regional capacity and such manipulations should focus on habitat quality rather than quantity.

In the future, management agencies must develop a comprehensive understanding of their stream resources over broad temporal and spatial scales (Naiman et al. 1993). We believe the hierarchial approach outlined in this paper promotes such an understanding. Use of sophisticated technologies (e.g., geographic information systems, remote sensing, and satellite imagery) should enhance spatiotemporal investigations of fish-habitat relations. Furthermore, the ability of these technologies to combine complex environmental, social, and economic variables will aid in developing the resource policies necessary for effective stream restoration and conservation.

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Relations among riparian grazing, sediment loads, macroinvertebrates, and fishes in three central Pennsylvania streams

Neil E. Wohl and Robert F. Carline

Abstract: We assessed relations among riparian grazing, sediment loads, macroinvertebrates, and fishes in three streams in adjacent catchments in central Pennsylvania. The catchments consisted mostly of agricultural and forest lands. Lengths of streams subjected to riparian grazing were 2.5 km along Cedar Run and 4.1 km along Slab Cabin Run; there was no riparian grazing along Spring Creek. Median daily discharge and temperatures during summer and winter were significantly different among streams. Annual sediment yields were 113, 255, and 273 t in Spring Creek, Cedar Run, and Slab Cabin Run, respectively. Substrate permeability of potential spawning sites for brown trout (*Salmo trutta*), and densities of benthic macroinvertebrates were significantly higher in Spring Creek than in the other streams. Densities of wild brown trout were 5-23 times higher in Spring Creek than in Cedar Run and Slab Cabin Run. Although there were marked differences among streams with and without riparian grazing, other watershed attributes could have had some influence on these streams.

Résumé : Nous avons évalué les relations existant entre le broutage riverain, la charge de sédiments, les macro-invertébrés et les poissons, dans trois petits cours d'eau de bassins-versants voisins, dans le centre de la Pennsylvanie. Ces bassins-versants étaient principalement recouverts de terres agricoles et de forêts. Le broutage riverain touchait 2,5 km du Cedar Run et 4,1 km du Slab Cabin Run, alors que les berges du ruisseau Spring n'étaient soumises à aucun broutage. Le débit quotidien moyen ainsi que les températures estivales et hivernales étaient sensiblement différents selon les cours d'eau. La production annuelle de sédiments était de 113 t pour le ruisseau Spring, de 255 t pour le Cedar Run et de 273 t pour le Slab Cabin Run. La perméabilité des substrats pouvant servir de frayères à la truite brune (*Salmo trutta*) et la densité des macro-invertébrés benthiques étaient significativement plus élevées dans le cas du ruisseau Spring que dans celui des deux autres cours d'eau. De même, la densité des truites brunes sauvages était 5–23 fois plus élevée dans le ruisseau Spring que dans le Cedar Run et le Slab Cabin Run. Il existe donc des différences marquées entre les cours d'eau soumis et non soumis au broutage riverain, mais il est possible que d'autres caractéristiques des bassins-versants aient eu une incidence sur ces cours d'eau.
[Traduit par la Rédaction]

Introduction

Livestock grazing in riparian zones has been linked to instream habitat degradation and salmonid recruitment failures. Removal of riparian vegetation increases variability in stream discharge, water temperature, and sediment loads (Barton and Taylor 1985; Cunjak and Power 1986; Hillman and Griffith 1987). Variable discharges in degraded streams may cause salmonid recruitment failures. Sando (1981) determined that large flow fluctuations in a Montana river resulted in complete mortality of eggs in 90% of redds. High turbidities also contribute to poor salmonid health and slowly alter salmonid microhabitat (Tappel and Bjornn 1983; Sigler et al. 1984; Redding et al. 1987; Chapman 1988).

It is difficult to compare effects of grazing and associated non-point-source pollution on streams in the Pacific Northwest and the Intermountain West to those in the humid East, primarily because vegetative cover in the East mutes denudation processes (Ritter 1986). Sediment losses in the West are characterized by high turbidities relative to discharge, whereas in the East, much greater discharges are needed to produce comparable turbidities (Wilson 1977). The lack of studies on effects of riparian grazing on stream biota in the East provided the impetus for this project.

We conducted this study in the Spring Creek watershed, central Pennsylvania, where earlier studies showed that poor recruitment of brown trout (*Salmo trutta*) in sections of Spring Creek was due to high sediment loads originating from two tributaries draining agricultural basins (Beard and Carline 1991). We assessed conditions in two streams with extensive riparian grazing and in a third stream with no riparian grazing. Our objectives were to document streamflow, sediment load, and substrate composition, and relate density and diversity of macroinvertebrate and fish communities to differences among streams.

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Materials and methods

The Spring Creek watershed (381 km^2), which lies within the Ridge and Valley physiographic province of central Pennsylvania (Fig. 1), drains into Bald Eagle Creek, a tributary to the West Branch of the Susquehanna River. Much of the stream water comes from limestone aquifers (Giddings 1974); hence, pH (7.7–8.4) and alkalinity (ca. 200 $mg \cdot L^{-1}$ as $CaCO_3$) are relatively high. Average precipitation in the basin is about 102 $cm \cdot year^{-1}$. During this study, 1991 was the

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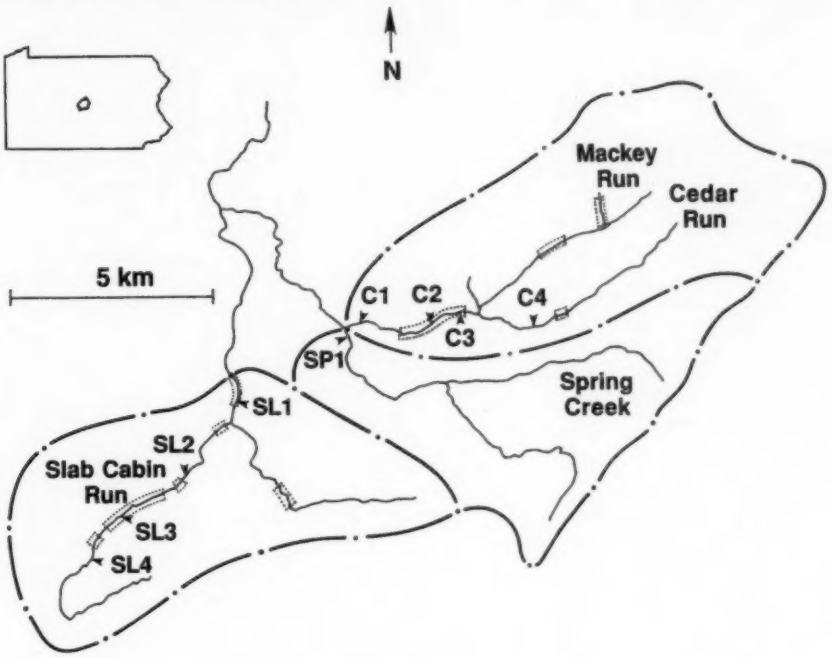
Fig. 1. Spring Creek watershed in central Pennsylvania and boundaries of three catchments with designations for fish and benthos sampling sites. Locations of riparian pasture >200 m long are highlighted.



driest year since 1931 and precipitation in 1992 was near average (NOAA 1991–1992).

Slab Cabin Run (Fig. 1) is 14.4 km long, drains 44 km^2 of agricultural (55%) and forest lands (43%), and receives treated wastewater from a treatment facility near the headwaters. A wellfield, located adjacent to the stream about 5.5 km below the stream's source, supplies about 6.62 million liters per day of potable water. About 4.1 km of the stream flows through unfenced pastures, where nearly the entire streambank is eroding.

Cedar Run is 7.9 km long and drains a 46 km^2 basin that is 85% agricultural, and the remainder is forestland. About 60% of Cedar Run and its main tributary, Mackey Run, flow through 2.5 km of unfenced pasture. Some of the pastured streambank has been stabilized with riprap and about 50% of it is eroding.

The upper segment of Spring Creek, starting at its confluence with Cedar Run, is about 6 km long and drains 34 km^2 of approximately equal areas of agriculture, forestland, and urban development. There are no riparian pastures in the catchment.

Continuous stream stage recorders were installed at the downstream boundaries of each basin in August 1991 (Fig. 1). At least 20 measurements of stream discharge were made at a wide range of stages in each stream. Quadratic regression equations ($r^2 > 0.99$) were used to convert water-level data to discharge. Temperature recording devices were placed on the streambed at each of the gauging stations and temperatures were recorded hourly.

We collected weekly water samples at each gauging site during baseflow, and we used automatic water samplers (ISCO) that were programmed to begin several hours before storm events were anticipated. During storms, samples were collected at 3-h intervals; during summer months when storms were of short duration, samples were taken at 1-h intervals. Between September 1991 and August 1992 we collected samples during 75% of the storms. We analyzed 240 samples for turbidity, in nephelometric turbidity units (NTU), with a Hach Portalab Turbidimeter (Model 16800) and 95 for total suspended solids (TSS) by filtering (0.45 μm), drying, and weighing them (American Public Health Association et al. 1989). A quadratic regression of turbidity versus TSS was developed to estimate TSS of samples for which only turbidity was measured.

We employed a linear interpolation method to estimate sediment loads. We used either single daily observations of TSS or a mean for all samples collected during a 24-h period and interpolated between days for which TSS measurements were made. Total daily discharge was multiplied by observed or estimated TSS to estimate daily sediment load.

We established one sampling station in Spring Creek, four in Cedar Run and four in Slab Cabin Run (Fig. 1), to characterize stream morphology, substrate composition, benthos, and fish communities; station lengths averaged 250 m. We sampled at only one station (ungrazed) in Spring Creek, because during dry periods much of the streamflow percolates into the streambed about 1 km upstream of its confluence with Cedar Run. Groundwater emerges about 500 m upstream from the confluence, upstream of where our station was located. Stream length with perennial flow at this location was considered insufficient for establishment of more than one sampling site. In both Cedar Run and Slab Cabin Run, two sampling stations were located in heavily pastured fields and two were in ungrazed fields with well-vegetated streambanks.

We measured water depth and velocity at 10–15 points along 9–14 transects at each of the sampling stations and characterized substrate size in July 1992 and 1994. Transects were spaced one stream width apart. The streambank at each end of the transect was classified as stable or eroding. Eroding streambanks had steep or vertical slopes with no vegetation. In May 1992, we used a 15 cm diameter stovepipe sampler (McNeil and Ahnell 1964) to collect substrates from sites that had a depth, velocity, and substrate size similar to those used for spawning by brown trout (Beard and Carline 1991). Four samples were taken from each of the nine stations, dried, and sieved through a series of 12 screens with openings ranging from

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Table 1. Channel characteristics of grazed and ungrazed reaches of Spring Creek, Cedar Run, and Slab Cabin Run.

Stream and station	Mean width (m)	Mean depth (cm)	Mean velocity ($cm \cdot s^{-1}$)	Discharge ($m^3 \cdot s^{-1}$)	Eroding streambank (%)	Substrate (%)		
						Silt-sand	Gravel	Cobble
Spring Creek								
Ungrazed								
SP1	5.6	21	17	0.197	10	4	17	79
Cedar Run								
Ungrazed								
C1	8.1	18	20	0.248	0	5	59	36
C4	6.3	22	12	0.159	10	36	60	4
Grazed								
C2	6.6	31	14	0.225	48	52	8	40
C3	6.4	21	19	0.223	59	33	34	33
Slab Cabin Run								
Ungrazed								
SL2	4.3	21	11	0.085	12	82	17	1
SL4	2.4	11	17	0.042	0	6	76	18
Grazed								
SL1	7.4	12	12	0.104	100	57	11	32
SL2.5[a]	4.9	21	4	0.046	100	90	0	10
SL3	2.5	19	10	0.051	100	82	1	17
Means of all sites								
Ungrazed	5.34	18.6	15.4	0.146	6.4[b]	26.6	45.8[b]	27.6
Grazed	5.56	20.8	11.8	0.130	81.4	62.8	10.8	26.4

Note: Measurements were made in summer 1992 and 1994.

[a]Midway between SL2 and SL3.

[b]Ungrazed versus grazed reaches significantly different (Kruskal-Wallis test, $P < 0.05$).

0.25 to 12.7 mm. The percentage by weight of material retained by each sieve was used to calculate the geometric mean particle size and the sorting coefficient, which is a measure of the size distribution of sediment particles. The Fredle index, which is the ratio of geometric mean particle size to sorting coefficient, provides a measure of substrate permeability (Lotspeich and Everest 1981).

We collected benthic macroinvertebrates from riffles using Surber samplers in June and August 1992; three samples per station were collected each time. Samples were sorted and identified to family. The frequency and abundance of taxa in each sample were analyzed with a Shannon diversity index (Pielou 1984).

We used direct current (200 V) electrofishing gear to inventory fish communities in May and August 1992. Trout densities were estimated at all nine sites by using the Zippin successive removal method (Zippin 1958) in a 250-m reach. All trout were weighed to the nearest gram, measured to the nearest millimeter, and released. Age-0 brown trout were readily distinguished from age-1 and older brown trout (hereafter referred to as age-1+) by examination of length-frequency distributions. We used software developed by Van Deventer and Platts (1989) to estimate densities and 95% confidence intervals for age-0 and age-1+ brown trout. These age-1, age-0 changes are global changes. When the computed lower 95% confidence interval was less than the total number caught, we used the total catch as the lower confidence interval. We carefully electrofished a subsection (50 m) of each sample reach and attempted to collect all species observed; these data were used to characterize fish communities.

Results

Stream morphology

Stream width and depth were similar among grazed and ungrazed stations and among streams (Table 1). The most striking difference among sampling stations was the nearly complete lack of woody vegetation in the riparian zone of pastured reaches. In ungrazed reaches, the streambank was vegetated with a mixture of grasses, shrubs, and trees. About 6% of the ungrazed streambanks were eroded in contrast to about 81% in grazed areas. In ungrazed reaches, there was significantly less silt and sand substrates and more gravel than in grazed reaches.

Stream hydrology

There was a significant difference (Kruskal-Wallis test, $P < 0.001$) in median discharge among streams; Spring Creek had the highest discharge and Slab Cabin Run, the lowest (Table 2). Slab Cabin Run had the most variable discharge and Cedar Run was the least variable. Runoff from a nearby highway interchange contributed to peak discharges in Spring Creek. Total daily discharge per unit basin area in Spring Creek was three times that in Cedar Run and about five times higher than in Slab Cabin Run. Wellwater withdrawals from the Slab Cabin Run basin probably reduced streamflows, because these withdrawals were about 0.75 times the median daily discharge.

Median daily TSS was significantly different (Kruskal-Wallis test, $P < 0.001$) among streams; it was lowest in Spring Creek and about seven times higher in Slab Cabin Run (Table 2). Annual sediment yield was lowest in Spring Creek and more than twice as high in Cedar Run and Slab Cabin Run. When annual water yield and basin area are taken into account, sediment yield in Slab Cabin Run was highest, nearly five times greater than in Spring Creek.

Temperature

Stream temperatures were largely a function of discharge.

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Table 2. Daily discharge, concentration of total suspended solids (TSS), and sediment yield of Spring Creek, Cedar Run, and Slab Cabin Run, September 1991 to August 1992.

Stream and statistic	Median daily discharge ($m^3 \cdot s^{-1}$)	Total daily discharge ($m^3 \cdot km^{-2} \cdot d^{-1}$)	Median daily TSS ($mg \cdot L^{-1}$)	Annual sediment yield: tonnes	Annual sediment yield: t·million $m^{-3} \cdot km^{-2}$
Spring Creek					
Median	0.38	953	5		
Range	0.16–2.61		1–260		
Total				113	0.24
Cedar Run					
Median	0.19	349	25		
Range	0.11–0.99		7–486		
Total				255	0.70
Slab Cabin Run					
Median	0.10	192	37		
Range	0.004–3.63		6–1237		
Total				273	1.15

Note: Median daily discharge and TSS were significantly different among streams (Kruskal-Wallis test, $P < 0.001$).

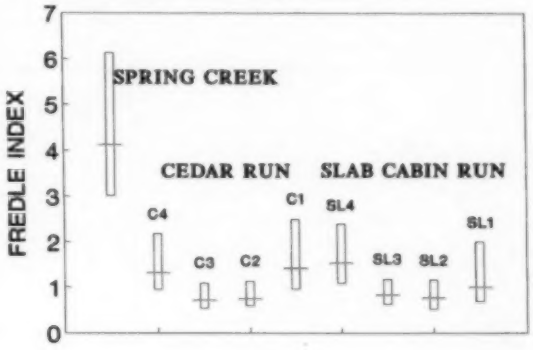
Table 3. Water temperatures (°C) of Spring Creek, Cedar Run, and Slab Cabin Run, September 1991 to August 1992.

Stream	Mean daily range	Instantaneous maximum	January daily median	August daily median
Spring Creek	3, 13.8	17.8	7.4	11.3
Cedar Run	(–0.5, 23.0	25.6	4.6	15.6
Slab Cabin Run	–0.3, 21.3	27.8	0.25	16.2

Note: Median temperatures in January and August were significantly different among streams (Kruskal-Wallis test, $P < 0.001$).

Spring Creek, which had the highest discharge, had the narrowest range of mean daily temperatures, the lowest instantaneous maximum temperature, the warmest temperatures in January, and the coolest in August (Table 3). Cedar Run was intermediate among streams with respect to discharge and temperature, while Slab Cabin Run had the lowest discharge and the most extreme temperatures.

Fig. 2. Median and range of Fredle index values for potential brown trout spawning sites in Spring Creek, Cedar Run, and Slab Cabin Run, June 1992. Four substrate samples were collected at each site, whose designation corresponds to Fig. 1.



Substrate composition

Substrate composition of potential trout spawning sites varied among streams, but not among stations (Fig. 2). The median Fredle index of substrates in Spring Creek (4.12) was significantly different (Kruskal-Wallis test, $P < 0.01$) than the median index in Cedar Run (0.97) and Slab Cabin Run (0.98). Fredle indices among stations were not significantly different ($P > 0.05$) in either Cedar Run or Slab Cabin Run. Thus, substrate permeability in Spring Creek was substantially higher than in the two streams with extensive streambank grazing.

Benthic macroinvertebrates

Benthic communities differed among streams. The dominant taxa in Spring Creek were amphipods and dipterans, which were mostly Chironomidae (Table 4). Isopods, amphipods, and dipterans were the dominant taxa in Cedar Run while dipterans were most abundant in Slab Cabin Run. There were no trends in median number of taxa found in the three streams. In May and August, Spring Creek had significantly ($P < 0.05$) greater numbers of benthic macroinvertebrates than the other two streams, where densities were not significantly different ($P > 0.05$). In May the Shannon diversity index was significantly ($P < 0.05$) higher in Cedar Run than in the other two streams, but in August there were no differences in diversity.

Fish populations

Fish communities were similar among stations within streams. We found only four fish species in Spring Creek and Cedar Run; slimy sculpins were the most abundant followed by brown trout (Table 5). In Slab Cabin Run we collected 12 species of which longnose dace, common white suckers, and slimy sculpins were the most numerous. The bluegills in Cedar Run and the banded killifish in Slab Cabin Run are not normally found in coldwater streams in this region.

Densities of age-1+ brown trout were judged significantly different among streams, because 95% confidence intervals of population estimates did not overlap (Table 6). In Spring Creek, May and August estimates ranged from about $1200 \cdot ha^{-1}$ to $1900 \cdot ha^{-1}$, which were approximately 5 times greater than the average density in Cedar Run and 22 times greater than that in Slab Cabin Run. Similarly, in August, density of age-0 brown trout in Spring Creek was about 13 times greater than the mean density in Cedar Run and 23 times

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Table 4. Composition of macroinvertebrate communities and median number of taxa, density, and diversity in Spring Creek, Cedar Run, and Slab Cabin Run, May and August 1992.

	Spring Creek		Cedar Run		Slab Cabin Run	
	May	August	May	August	May	August
Taxa (%)						
Amphipoda	61	56	17	17	2	14
Isopoda	0	0	30	22	1	1
Coleoptera	3	5	2	11	[a]	1
Diptera	21	29	21	35	70	47
Ephemeroptera	3	3	1	1	1	2
Trichoptera	7	5	14	11	2	16
Oligochaeta	2	[a]	6	[a]	22	10
Turbellaria	3	[a]	1	1	1	5
Other	[a]	2	8	2	1	3
Median number of taxa	17		11.5		10	
		14		13.5		14.5
Density (no.·m^{-2})	17 980*x*		4422*y*		3944*y*	
		15 279*x*		6838*y*		4100*y*
Diversity index	1.19*x*		1.81*y*		1.19*x*	
		1.32*x*		1.60*x*		1.61*x*

Note: Density and diversity values in rows followed by the same letter were not significantly different (Kruskal-Wallis test, $P > 0.05$).

[a]Less than 0.5% of total number.

Table 5. Percentage composition of fish communities in Spring Creek, Cedar Run, and Slab Cabin Run, May and August 1992.

	Percent of total number collected		
	Spring Creek	Cedar Run	Slab Cabin Run
Brown trout (*Salmo trutta*)	26.1	13.3	1.4
Slimy sculpin (*Cottus cognatus*)	72.0	75.4	10.5
White sucker (*Catostomus commersoni*)	1.4	11.1	30.5
Longnose dace (*Rhinichthys cataractae*)			37.7
Blacknose dace (*Rhinichthys atratulus*)	0.5		3.3
Creek chub (*Semotilus atromaculatus*)			2.4
Fallfish (*Semotilus corporalis*)		<0.1	
Pearl dace (*Margariscus margarita*)			0.1
Common shiner (*Luxilus cornutus*)			0.3
Fathead minnow (*Pimephales promelas*)			8.5
Tessellated darter (*Etheostoma olmstedi*)			0.8
Bluegill (*Lepomis macrochirus*)		0.2	
Banded killifish (*Fundulus diaphanus*)			4.4

Note: Data were combined from all stations for both months.

greater than that in Slab Cabin Run. In Cedar Run the variation in trout density was not related to grazing, but in Slab Cabin Run the highest density was found in an ungrazed reach (SL4), which had little agricultural activity upstream of it.

Discussion

Results of this study of stream reaches subject to intensive riparian grazing are generally consistent with other published studies. Although the focus here was on conditions of the riparian zones, stream morphology, hydrology, sediment loads, and biotic communities reflect the cumulative effects of conversion of forestland to agriculture, urban and infrastructure development, and groundwater withdrawals. While it is impossible to ascribe differences in communities to specific watershed attributes, an examination of conditions among streams allows us to make some inferences about causative factors.

Streamflows differed significantly among sites and low flows in Slab Cabin Run may have contributed to the sparse trout population. Groundwater withdrawals in Slab Cabin Run undoubtedly reduced streamflow, which was most apparent during the 1988 drought when flows between pools were negligible. In contrast, the Spring Creek site supported a high density of trout during this drought (Beard and Carline 1991). It is likely that Slab Cabin Run would not support as large a trout population as Spring Creek, even if riparian grazing in the Slab Cabin Run basin was completely eliminated.

Differences in water temperature among streams was probably related to several factors. The absence of riparian shading in large sections of Cedar Run and Slab Cabin Run must have contributed to high summer temperatures (Gorman and Karr

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Table 6. Estimated densities (95% confidence intervals in parentheses) of age-0 and age-1+ brown trout in Spring Creek, Cedar Run, and Slab Cabin Run, May and August 1992.

Stream and station	May		August	
	Age group	Estimate (no.·ha^{-1})	Age group	Estimate (no.·ha^{-1})
Spring Creek			0	3512 (702, 18 012)
	1+	1893 (1892, 2250)	1+	1238 (988, 1560)
Cedar Run				
C1			0	269 (170, 526)
	1+	363 (363, 368)	1+	170 (169, 181)
C2			0	336 (244, 756)
	1+	513 (513, 529)	1+	672 (647, 723)
C3			0	409 (372, 474)
	1+	255 (255, 277)	+1	197 (197, 212)
C4			0	36 (35, 43)
	1+	129 (129, 137)	1+	94 (94, 108)
Mean			0	263
	1+	315	1+	283
Slab Cabin Run				
SL1			0	0
	1+	15 (15, 31)	1+	15 (15, 31)
SL2			0	0
	1+	35 (35, 70)	1+	35 (35, 70)
SL3			0	0
	1+	48 (48, 96)	1+	48 (48, 96)
SL4			0	599 (599, 790)
	1+	136 (136, 218)	1+	245 (245, 327)
Mean			0	150
	1+	59	1+	86

1978; Claire and Storch 1983; Yankey et al. 1991). Streamflow and proximity of monitoring sites to sources of groundwater inputs were also important. Spring Creek, where temperature varied least, had the highest streamflow and a large groundwater inflow was less than 1 km upstream of the monitoring site. Cedar Run had substantially more streamflow than Slab Cabin Run and less extreme temperatures in summer and winter. We do not believe that the relatively high summer temperatures in Slab Cabin Run adversely influenced the brown trout population, because in sections of Spring Creek about 22 km downstream of the Spring Creek – Cedar Run confluence, summer temperatures exceed those in Slab Cabin Run yet trout densities are among the highest in the entire watershed (R. Carline, unpublished data).

Channel morphology was not substantially different among and within streams. Large woody debris, which has been positively correlated with salmonid density (Elliott 1986), was scarce in both ungrazed and grazed reaches. This was not unexpected in the grazed reaches, where woody vegetation was absent from the riparian zone. The lack of large woody debris in ungrazed sections was probably due to the young age of trees in the riparian zone and the relatively long distances (5–10 km) from forestlands in the extreme upstream portions of these catchments. The most notable differences among grazed and ungrazed reaches were the amount of eroding streambank and the predominance of fine substrates in the streambed.

Yankey et al. (1991) conducted a 10-year study on nonpoint-source pollution in Rock Creek, Idaho, and concluded that eroded streambanks in grazed areas were a major source of sediment. They estimated that at least 48% of streambank length in Rock Creek, similar to our estimates for Cedar Run and Slab Cabin Run, was eroded. They also estimated that sediment from grazed areas was two to five times greater than that from croplands. We did not attempt to quantify the sources of sediment; hence, we cannot assess the relative contributions of streambanks and cropland to total sediment yields.

Differences in sediment loads and substrate composition among streams seemed to account for at least some of the differences in benthic communities. Densities of benthic organisms were highest in Spring Creek where sediment loads were lowest. Macrobenthos density declines with increasing sediment loads and reduced substrate size (Rabeni and Minshall 1977; Minshall 1984). The shift in dominance from amphipods in Spring Creek to chironomids in Slab Cabin Run is also consistent with observations of streams in forested and agricultural catchments (Dance and Hynes 1980). However, densities of ephemeropterans and trichopterans, which are sensitive to changes in water quality (Lenat 1984), did not demonstrate consistent trends among streams.

Substrate composition probably had a direct effect on brown trout by influencing reproductive success. Beard and Carline (1991) found that the Fredle index of trout spawning sites in the mainstem of Spring Creek was substantially higher (3.0–4.1) than in Cedar Run (0.97) and Slab Cabin Run (0.98), where few age-0 trout were found. The Fredle index in our Spring Creek station (4.1) was comparable with sites farther downstream, where embryo survival was high. Providing that our selection of potential spawning sites for substrate analyses was representative, we would predict that embryo survival in Cedar Run and Slab Cabin Run would be low. It is possible that spawning activity in these streams could alter substrate composition and result in higher Fredle indices than we measured. Nonetheless, it has been convincingly demonstrated that increases of fine materials in salmonid spawning sites reduce embryo survival (for review see Chapman 1988).

Though differences in recruitment among streams could readily account for differences in density of age-1+ brown trout, other factors may have played a role. Invertebrate food resources, which were clearly higher in Spring Creek than in the other streams subjected to grazing, may have contributed to differences in trout density among streams. Another appar-

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ent habitat difference was the lack of overhanging bank vegetation in the grazed sections in contrast to ungrazed ones, where grasses and shrubs provided a substantial amount of cover along the banks. Aquatic vegetation and grass cover along banks are regarded as important habitat features of productive trout streams (Hunt 1979).

The relatively simple fish communities found in Spring Creek and Cedar Run are typical of first- and second-order coldwater streams in this physiographic province. As stream order and water temperatures increase, fish diversity increases. This pattern is also common in western U.S. streams; Decker and Erman (1992) also found that fish diversity increased with increasing temperature. Fish diversity was highest in Slab Cabin Run, which had the warmest summer temperatures.

For the most part, differences among catchments with intensive riparian grazing and the reference site were rather striking. Our results are consistent with findings from a large number of studies in western United States (Armour et al. 1991). We conclude that riparian grazing along streams in the East has effects similar to those in the West, despite major climatic differences. Further studies on grazing effects in the East should document how stream ecosystems respond to habitat restoration of intensively grazed riparian zones.

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Winter habitat of selected stream fishes and potential impacts from land-use activity

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Abstract: This paper reviews the habitat characteristics and the behaviour of selected stream fishes during winter in temperate–boreal ecosystems. Emphasis is placed on the salmonid fishes upon which most winter research has been directed. As space is the primary factor regulating stream fish populations in winter, aspects of winter habitat are considered at various spatial scales from microhabitat to stream reach to river basin. Choice of winter habitat is governed by the need to minimize energy expenditure, with the main criterion being protection from adverse physicochemical conditions (e.g., ice, spates, low oxygen). The distance moved to wintering habitats, and the continued activity by many fishes during winter, need to be considered when making management decisions regarding fish habitat. How habitat is affected by land-use activity in stream catchments is discussed with reference to impacts from water withdrawal, varying discharge regimes, and erosion or sedimentation. Even stream "enhancement" practices can deleteriously affect fish habitat if project managers are unaware of winter habitat requirements and stream conditions. Maintenance of habitat complexity, at least at the scale of stream sub-basin, is recommended to ensure the diversity of winter habitats for fish communities.

Résumé : Le document fait l'examen des caractéristiques de l'habitat et du comportement de certains poissons de cours d'eau pendant l'hiver en écosystèmes tempérés ou boréaux. L'accent est mis sur les salmonidés qui ont fait l'objet de la plus grande partie des recherches effectuées en hiver. L'espace étant le premier facteur régissant les populations de poissons de cours d'eau en hiver, les aspects de l'habitat d'hiver sont examinés en fonction de diverses échelles spatiales allant du micro-habitat, au segment et au bassin du cours d'eau. Le choix de l'habitat d'hiver est régi par le besoin de minimiser les dépenses énergétiques et a pour critère principal la protection contre les conditions physiques et chimiques adverses (glaces, crues, faible teneur en oxygène). La distance parcourue pour atteindre les habitats d'hivernage et le maintien de l'activité d'un grand nombre de poissons pendant l'hiver doivent être pris en compte au moment de la prise de décisions de gestion touchant l'habitat du poisson. La façon dont l'habitat est affecté par l'utilisation des terres dans le bassin du cours d'eau est traitée dans le contexte des incidences de la captation d'eau, de la variation des régimes d'écoulement, de l'érosion et de la sédimentation. Même les activités de «mise en valeur» des cours d'eau peuvent altérer l'habitat du poisson si les gestionnaires de projet ne tiennent pas compte des besoins en habitats d'hiver et des conditions du cours d'eau. Le maintien de la complexité de l'habitat, du moins à l'échelle du sous-bassin du cours d'eau, est recommandé pour garantir la diversité des habitats d'hiver des communautés de poissons.
[Traduit par la Rédaction]

Introduction

"We had not thought seriously of winter; we dwelt in fancied security yet"

Henry David Thoreau (circa 1850)

In the past decade, the number of publications focusing on the winter ecology of stream fauna has increased (e.g., Cunjak and Power 1986*a*; Brown and McMahon 1988; Ultsch 1989; Griffith and Smith 1993; Heggenes et al. 1993; Irons et al. 1993; Scrimgeour et al. 1994). Although these studies have contributed to an improved understanding of habitat use and behaviour of stream fishes during winter, much remains to be learned. The need to understand, identify, and quantify the winter habitat of fishes during all life stages is an obvious prerequisite to successful fisheries management. This requirement is all the more urgent given the potential impacts and complications imposed by anthropogenic perturbations in stream catchments (see Power et al. 1993) and the demands for land-use activity, which are increasing.

This paper reviews the winter habitat characteristics and the winter behaviour of selected stream fishes, particularly those common to the streams of the Great Lakes drainage. My goal is to identify the critical characteristics of winter habitat to ensure their protection and, hence, conservation. Emphasis is given to salmonid fishes upon which most research has been directed. I will restrict my review to running waters and will only make limited reference to lacustrine environments as wintering areas recognizing, however, their significance for many stream fishes (Cederholm and Scarlett 1982; Peterson 1982; Hutchings 1986). Winter diet, metabolism and energetics, and the habitat of pre-emergent fish (i.e., overwintering eggs, alevins) are also not included in this review. The paper concludes with a section describing potential impacts to winter habitat from land-use activity in stream catchments. Largely speculative given our current ignorance of biotic responses to anthropogenic perturbations in winter, this section suggests that maintenance of habitat complexity, at least at the scale of stream sub-basin, is needed to satisfy the diverse habitat requirements of lotic fish communities in winter.

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Table 1. Generalized criteria for winter habitat selection by fishes in natural, coldwater streams, listed in order of relative importance (priority).

Relative priority[a]	Habitat criterion	Example(s) of selected habitat
1	Protection from adverse physicochemical conditions (e.g., ice, low oxygen, winter freshets), and access to refugia or alternate winter habitats	Suitable water depth, instream cover, floodplain habitat and side-channels, source of aeration, groundwater discharge zones, subice corridors
2	Protection from predators	Suitable water depth, instream cover
3	Access to food	Low-velocity (micro)habitats and concomitant shift to nocturnal, benthic feeding pattern

[a]Relative priorities can vary among life stages and for different streams depending on availability of food, on water temperature (and metabolic demand), on local predator density, and on the stability of environmental conditions.

Winter is herein described as that period immediately following egg deposition by autumn-spawning salmonids (and coincident with a decline in water temperature) and extending until the loss of all surface ice (often accompanied by a major spate and snowmelt) and prior to any reproductive activity by spring-spawning, non-gadid fishes. This definition, considered to have more biological relevance than one following calendar dates, has been modified from one suggested by Cunjak and Power (1986*a*). The streams reviewed in this paper are those subject to near-freezing temperatures (<1°C) or ice formation for some portion of the winter period (such that growth over winter is considered negligible). The winter habitat of fishes in warmwater streams is not considered here, although there is a corresponding lack of information from these environments, and for the unique strategies employed by resident species (e.g., *Cyprinodon* spp.; McMahon and Tash 1988).

Characteristics of preferred winter habitat

Space, specifically suitable physical habitat features (e.g., low-velocity areas, instream cover), is the primary factor regulating stream fish populations in winter because reduced metabolic demands at low water temperatures lessen, or eliminate, time spent feeding and defending territories (see Chapman 1966). Cunjak and Power (1986*a*) suggested that the specific choice of winter habitat, and the behavioural pattern adopted by stream-dwelling brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in winter, was governed by the basic need to minimize energy expenditure. This was accomplished by selecting positions in low-flow microhabitats with suitable cover and physicochemical attributes, but where predation risk and energy depletion were minimized. The concept that winter habitat selection is based on minimizing energy expenditure has been proposed for other juvenile salmonid species (Bustard and Narver 1975*a*; Rimmer et al. 1984; Cunjak 1988*a*; Griffith and Smith 1993; Riehle and Griffith 1993), and for smallmouth bass (*Micropterus dolomieu*; Todd and Rabeni 1989), largemouth bass (*Micropterus salmoides*; Carlson 1992), and blacknose dace (*Rhinichthys atratulus*; Cunjak and Power 1986*b*).

Assuming that the principal factor governing the choice of winter habitat is to minimize energy expenditure, I have prioritized criteria for winter habitat selection (Table 1). The same criteria could define fish habitat at other times of the year (except the reproductive period when fish also need access to suitable spawning habitat and mates). Rather, the difference in habitat selection criteria is in the relative priorities and particular environmental conditions inherent to winter compared with other seasons.

Protection from adverse physicochemical conditions

A variety of adverse conditions can develop in streams during winter. These include midwinter flood events, deoxygenation in ice-covered pools, de-watering of stream sections, ice blockages, and freezing temperatures. To survive, stream fishes have adopted specific habitat preferences where the probability of encountering adverse conditions is minimized. Two of these preferences, instream cover and groundwater discharge, are discussed in some detail.

Instream cover

Preferences for a particular type and structure of winter cover (as inferred from frequency of use data from field studies) differ among species (Table 2). Strongly photonegative (winter) species such as juvenile Atlantic salmon (*Salmo salar*), chinook salmon (*Oncorhynchus tshawytscha*), brown trout (Norway, Idaho), brook trout (Newfoundland, northern Quebec), rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Salmo clarki*), cottids, some cyprinids, and most centrarchids (and darters?) prefer sheltering beneath rubble–boulder where rock diameter is often directly proportional to the size of the fish beneath (Rimmer et al. 1984; Cunjak 1988*a*). Some of these fish may move 15–30 cm below the substrate surface (Everest 1969; Erkinaro et al. 1994; J. Thorpe, Freshwater Fisheries Laboratory, Scotland, personal communication). Brook trout and brown trout in the Credit River, Ontario, were rarely observed beneath rocks in winter, preferring instead positions beneath woody debris, undercut banks, and shelf ice, or within macrophyte mats (Table 2). Rocks and boulders were used as winter cover by other Credit River fishes such as mottled sculpin (*Cottus bairdi*), longnose dace (*Rhinichthys cataractae*), and blacknose dace (Table 2). Maciolek and Needham (1952) found that brown and rainbow trout frequently used shelf ice as cover in Convict Creek, California. Hillman et al. (1987) found wintering juvenile chinook salmon under cover of vegetated banks or cobble in an Idaho stream, whereas juvenile coho salmon (*Oncorhynchus kisutch*) were generally found to prefer pools and off-channel habitats with woody debris cover (Hartman 1965; Bustard and Narver 1975*a*), abundance being positively related to cover complexity (McMahon and Hartman 1989). Cover use can also change during the winter. Recently, Griffith and Smith (1995) observed that the density of young-of-the-year rainbow trout in macrophyte beds steadily declined between November and

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Table 2. Frequency of use of different types of cover by individual fishes in the Credit River system, Ontario, during winter (November–March) 1982–1985.

Species	Woody debris	Surface (shelf) ice	Cobble-boulders	Surface turbulence	Vegetation	Undercut bank	Depth > 1 m
Brook trout	119	4	3	4	67	60	2
Brown trout	17	6	2	13	9	3	0
Blacknose dace	0	0	81	1	0	0	0
Longnose dace	0	0	7	0	0	0	0
Mottled sculpin	0	0	28	0	0	0	0
White sucker (adults)	2	0	0	0	1	0	41
Bluegill	0	0	0	0	4	0	0
Pumpkinseed	1	0	2	0	3	0	0

Note: Frequencies are based on underwater observations.

January despite continued availability of the vegetation cover; instead, most of the trout overwintered in cobble–boulder substrate, where available.

Large-bodied, adult fish (e.g., salmonids, catostomids, centrarchids), probably because suitably sized rock shelters are scarce in many streams, generally overwinter in deep pools where depth is assumed to provide the requisite cover requirements. Adult white suckers (*Catostomus commersoni*), as solitary fish (Table 2) or in aggregations, overwintered in the deepest pools of the upper Credit River (Cunjak and Power 1986*a*). Carlson (1992) found that adult largemouth bass aggregated in a few deep, winter refuge areas in the Hudson River estuary where conditions permitted a minimum of energy expenditure. However, deep water does not necessarily imply suitable winter habitat. Cunjak and Caissie (1994) measured the accumulation of frazil ice in a large, main river (Miramichi) pool (55 105 m^3) in New Brunswick over two winters where it was generally believed post-spawned Atlantic salmon (kelts) overwintered. They found that, on average, frazil ice filled > 75% of the pool volume between December and March, and was often in contact with the pool bottom in the deepest part (8.7 m). The remaining pool space was assumed to be of marginal suitability because of the consequent higher water velocities deflected there by the frazil mass. More recent research in the Miramichi River has found that frazil ice also occurs in other large pools surveyed in the Miramichi River (D. Caissie, Department of Fisheries and Oceans, Moncton, N.B., unpublished data). In such cases, off-channel areas of river (e.g., braids, backwaters) may provide the habitat conditions necessary for overwintering fishes (i.e., free of frazil ice, adequate water depth, low water velocity as suggested from tracking radiotagged kelts, (R.A. Cunjak, unpublished data).

Groundwater discharge

Point sources of groundwater discharge which provide "winter-warm" microhabitats may serve as winter refugia (Table 1) from instream problems such as ice and variable streamflow. Cunjak and Power (1986*a*) found large numbers of brook and brown trout aggregated near such point sources in the headwaters of the Credit River in southern Ontario. Occasionally, pumpkinseed (*Lepomis gibbosus*) and cyprinids (such as blacknose dace) were also observed in such locations, actively swimming (Cunjak 1986*a*), which is not typical winter behaviour for these species. Known to be important thermal refugia during periods of high-temperature stress in summer (Gibson 1966; Snucins and Gunn 1995), point sources of groundwater discharge are now recognized for their importance as winter habitat. Swales et al. (1986) found that juvenile coho salmon in an interior British Columbia stream preferred to overwinter in side-channels and ponds where groundwater maintained warmer temperatures than in the main river. Craig and Poulin (1975) found stream populations of grayling (*Thymallus arcticus*) and arctic char (*Salvelinus alpinus*) overwintering in two perennial spring sections of an Alaskan river. In arctic systems, groundwater may be the most important winter habitat criterion (J.B. Reynolds, University of Alaska, Fairbanks, Alaska, personal communication) where, otherwise, streams can freeze completely. In temperate latitudes, the winter-warm conditions of groundwater discharge have been associated with increased winter survival of brook trout in Wisconsin (Hunt 1969); rainbow trout in Idaho (Smith and Griffith 1994); and juvenile steelhead, coho, and chinook salmon in British Columbia (Bustard 1986).

Proximity to the source of groundwater discharge, where water temperature is often warmest in winter, is not preferred by all species, even if cover is abundant. Brook trout, especially young individuals, typically prefer to position themselves close to point sources of groundwater. Brown trout, in contrast, do not and prefer to aggregate downstream from such sources, where water temperatures have cooled but still remain above freezing. Spatial variation between species is illustrated by plotting the abundance of individual (i.e., nonaggregated) trout during winter and the strength of the groundwater discharge (pressure head) as measured at three sites in the Credit River (Fig. 1). Brook trout abundance was positively related to strength of the discharge, whereas brown trout abundance was least at the site with greatest pressure head (Fig. 1) and where winter water temperature was highest (range 1.5–5.5°C). Avoidance by brown trout of such sources of undiluted, warmer groundwater was also noted by Hansen (1975) in a Michigan stream. Recently, R.A. Cunjak (unpublished data) found similar avoidance of spring sources by Atlantic salmon parr in several catchments in Prince Edward Island although brook trout were abundant. It may be that certain salmonid species are not physiologically adapted to effectively use the higher water temperatures in winter. The concomitant increase in metabolic activity at water temperatures between 5 and 7°C (as are often found near sources of groundwater discharge) would necessitate an increased feeding and assimilation efficiency. Not all fishes are metabolically efficient at such low water temperature. Instead, the advantages of the

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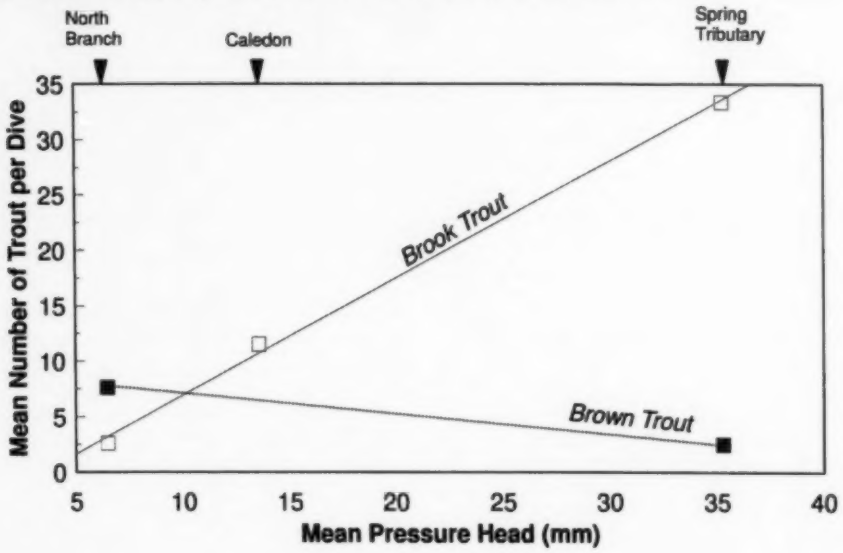
Fig. 1. Abundance of brook and brown trout observed during daytime underwater observations at three sites in the upper Credit River, Ontario (1983–1985), in relation to strength of groundwater discharge. Groundwater pressure (mm) was measured according to the technique outlined by Lee and Cherry (1978). Note that brown trout do not occur in the Caledon site.



groundwater warming may be better realized at a distance from the source, where ice formation is precluded and streamflow is still relatively stable, but where reduced water temperature (i.e., 2–4°C) would minimize metabolic activity. Alternatively, the local availability of certain physical habitat features (e.g., water depth, instream cover) and the specific habitat preferences of some salmonids may also explain the differential use of groundwater discharge zones. Such species-specific differences in winter habitat preferences may also reduce potential competition for space along a longitudinal gradient.

Hynes (1970, 1983) explained the importance of groundwater to stream ecosystems in general. More specifically, Meisner et al. (1988) hypothesized on the importance of groundwater as thermal refugia and how these may affect salmonid populations under the scenario of climate warming. Point sources of winter-warm water should be conserved. However, the appreciation and identification of groundwater discharge is not always obvious, especially if the discharge is small, diffuse, or in midstream. Detailed monitoring of water temperature at numerous points along a length of stream in midsummer or midwinter is one means of groundwater discharge identification. The location of open water and unfrozen sections of stream bank in midwinter often indicate groundwater, as do certain species of vegetation such as watercress (*Nasturtium officinale*) and eastern white cedar (*Thuja occidentalis*). Finally, if underwater observations are possible, winter (and summer) aggregations of juvenile salmonids are generally good indicators of groundwater discharge (Cunjak and Power 1986*a*).

Predator avoidance

Avoidance of predators and adverse physical conditions in the stream during winter (Table 1) is greatly influenced by a fish's swimming ability and its critical holding velocity, both of which are markedly reduced at low water temperature (Sandström 1983; Rimmer et al. 1985; Heggenes and Traaen 1988; Veselov and Shustov 1991; Bodensteiner and Lewis 1994). This is especially problematic for fishes trying to avoid endothermic predators (e.g., mink, otter, mergansers), which are known to be effective predators of overwintering fishes (Salyer and Lagler 1940; Alexander 1979; Carss et al. 1990) and which are not subject to the same temperature constraints to metabolism as are ectotherms. The problem may be compounded where suitable overwintering areas (e.g., pools, off-channel backwaters) are few, resulting in large concentrations, or aggregations, of overwintering fishes and may partly explain reports of substantial winter mortality (Bustard 1986; Dolloff 1993; Power and Mitchell 1994).

Access to food

Whereas feeding in summer is primarily the means to achieve surplus energy for growth and (or) reproductive maturity, winter feeding is often viewed as the way that fish, particularly young (juvenile) individuals, sustain a minimal level of metabolic activity (Cunjak 1988*b*) with negligible growth (e.g., Conover 1992; Metcalfe and Thorpe 1992). There are exceptions to this rule. Many spring-spawning fishes complete maturation in late winter (Tartar 1969; Lalancette 1973; Medford and Mackay 1978; Chilton et al. 1984). Atlantic salmon kelts resume feeding (and growth) in late winter (personal observations), and pre-smolt Atlantic salmon were found to continue growing in laboratory experiments (Metcalfe et al. 1988). In general, however, access to food at near-freezing water temperatures is probably a low-priority criterion for selection of winter habitat for most stream species (Table 1). Griffith and Smith (1993) estimated that only 61–66% of the juvenile cutthroat and brown trout overwintering in an Idaho

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Table 3. Generalized behavioural strategies employed by stream fishes for overwintering in temperate–boreal systems in North America.

Strategy	Tactics	Examples of fish taxa
Emigration to lentic habitats (e.g., lakes, estuaries)	Long-distance movement in late autumn or early winter	Arctic char, some *Oncorhynchus* spp., some adult Atlantic salmon
Active, stream resident	Shift to low-velocity habitats; behavioural changes (e.g., gregarious, nonterritorial, photonegative); continued feeding activity; substrate-hiding (daytime)	Most salmonids (especially juveniles), pike, cottids, some centrarchids, umbrids, and gadids
Inactive, stream resident	Shift to low-velocity habitats; some substrate-hiding; reduced metabolic activity (semitorpid?); minimal (sustenance) feeding	Catostomids, black-nosed dace, juvenile brook trout (sub-Arctic streams), darters, gasterosteids
Hibernation–torpor	Basal metabolism; fasting; "burrowers"	Many cyprinids, some centrarchids

river (water temperature approximately 7°C) emerged each night from beneath boulder concealment, presumably to feed. They suggested an even less frequent emergence in midwinter at lower water temperatures.

In many of our streams, invertebrate (food) abundance and biomass remain relatively high, particularly where winter-growing insect species (e.g., Plecoptera, some Ephemeroptera) are common (Hynes 1970). Assuming winter food availability and suitability are adequate (which has yet to be rigourously tested), I contend that the selection of winter habitat is primarily driven by the need to avoid adverse instream conditions and predation. Food, however, may become limiting to stream fishes in late winter following loss of potential prey individuals through death, emergence, or pupation–diapause. In this situation, or during a sudden rise in midwinter water temperature that may increase metabolic demand, access to food can become a relatively high priority habitat criterion (Table 1).

Winter habitat: aspect of scale

In dealing with conservation, or enhancement, of fish habitat, it is important to match habitat requirements to a scale and context appropriate to the range of that animal. Winter habitat data derived from one stream basin may be inappropriate for another area where different hydrologic conditions (Fig. 2) dictate alternate winter behaviour patterns by resident fishes. Stream fishes use different strategies for overwintering, depending on the species, life stage, and the availability of suitable habitats in the system (Table 3). I will consider aspects of winter habitat and behaviour at various spatial scales from the detailed characterization of microhabitats (fine scale) to the ecological conditions inherent to habitat types and stream reaches (medium scale). Large-scale considerations of winter habitat, which include whole river catchments, sub-basins, and landscape relationships, are discussed only with regards to long-distance movement between summer and winter areas.

Fine-scale habitat considerations

Focal-point measurements of microhabitat variables are routinely collected by fish ecologists in characterizing the microhabitat preferences of fishes (e.g., Cunjak and Green 1983; Fausch 1993; Cunjak and Power 1986*a*; Heggenes and Saltveit 1990; Hillman et al. 1987; Gibson 1988). Typical measured variables include focal point water velocity and water depth, mean water velocity (at 0.6 depth), total water depth, proximity to cover, type of cover, and substrate type. Often these data are subsequently used to construct habitat suitability index (HSI) curves for use in habitat simulation models such as IFIM-PHABSIM (Bovee 1982).

Maximum suitability and availability of winter microhabitats for resident stream fish communities is achieved where complexity of instream structure and form is conserved. Indeed, habitat quality may be more important than quantity in winter, as suggested by Todd and Rabeni (1989) in noting the relative importance to adult smallmouth bass of a few strategically placed boulders in a Missouri stream. Similarly, rubble-boulder shelters were critical winter habitats for stream salmonids and cyprinids (Bustard and Narver 1975*b*; Cunjak and Power 1986*b*; Cunjak 1988*a*; Griffith and Smith 1993; Hillman et al. 1987).

Microhabitat choice in winter may be a function of competition for similar shelters among stream-dwelling fishes (Cunjak and Power 1986*a*, 1986*b*), frogs (Cunjak 1986*b*), and invertebrates (e.g., crayfish). Hartman (1965) hypothesized that vertical partitioning of winter habitat (with steelhead juveniles preferring the stream bottom to the midwater positions preferred by coho salmon) was the result of competition. Heggenes et al. (1993) similarly suggested that intra- and interspecific competition among stream salmonids in winter may be severe because of more restricted habitat requirements. That winter space (i.e., habitat) may be limiting and the focus of competition among stream organisms seems probable, but still unproven, and deserves further attention.

The lack of information concerning the winter microhabitat requirements of non-salmonid species is an obstacle to effectively managing fish populations as multispecies assemblages or communities. Much of what we know is based on anecdotal evidence (e.g., Table 2). Generally, thick cover in the form of complex woody debris or rubble-boulders, or deep pools for larger adults, is preferred by most centrarchids, catostomids, and cyprinids (Webster 1954; Hasler and Wisby 1958; Paragamian 1981; Tallman and Gee 1982; Cunjak and Power 1986*b*; Pajak and Neves 1987; Todd and Rabeni 1989). Is there movement over winter; what is the frequency of emergence from winter shelters and do they feed; to what depth into the substrate do these fishes move to overwinter? These basic questions about microhabitat and behaviour remain unresolved for many stream fishes.

Medium-scale habitat considerations

Stream habitat, when viewed at the scale of habitat type (e.g., riffle, run) or stream reach, offers a variety of instream condi-

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Fig. 2. Differences in mean monthly stream discharge regimes for selected Canadian rivers from contrasting climatological regions. Solid bars represent typical winter months; hatched bars represent the spring–autumn period. Data for British Columbia streams (Sarita, Telkwa, Nanaimo, and Morice) were reproduced, with permission, from Bustard (1986); data for Upsalquitch River (northern New Brunswick) and the LaHave and Mersey rivers (southwestern Nova Scotia) were taken from Environment Canada gauge station records. Note that the Mersey River (natural) flow regime is from a station upstream from the regulated station. J, January; D, December.

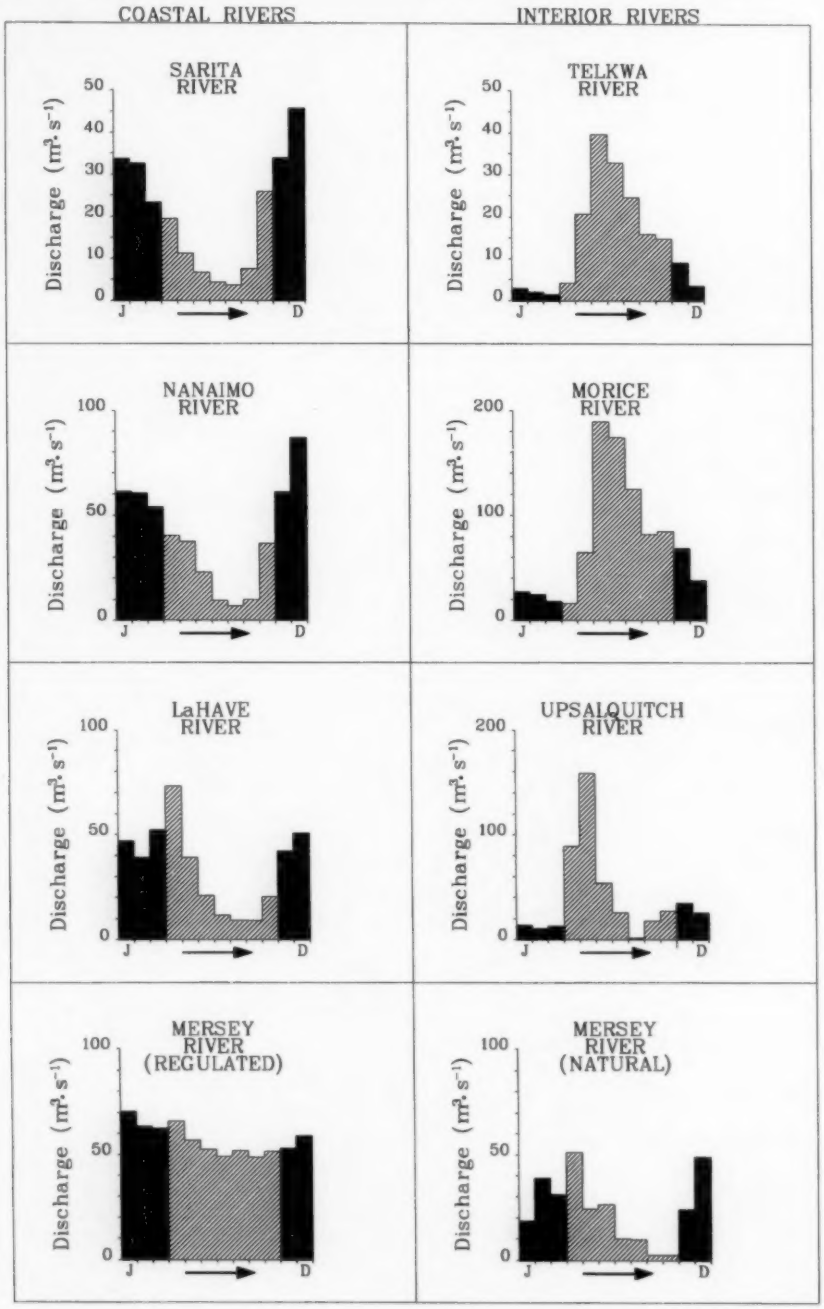

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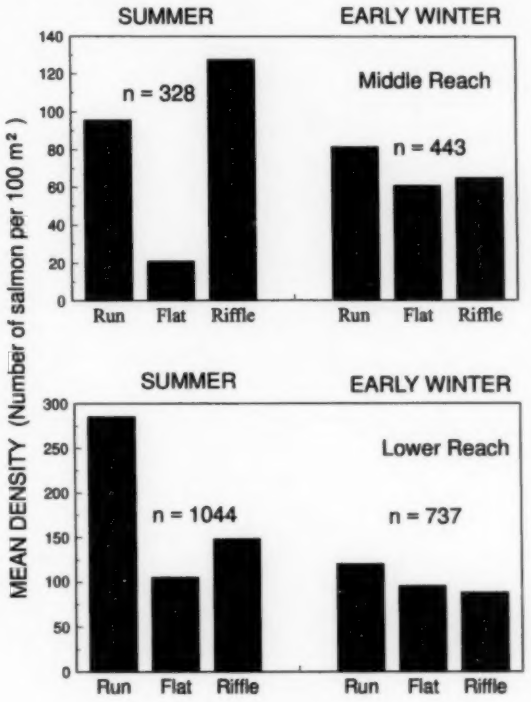
Fig. 3. Changes in mean density of juvenile Atlantic salmon (ages 0+ to 2+) from summer (July) to early winter (November) among different habitat types in two stream reaches of Catamaran Brook, New Brunswick, in 1991. Densities are averages of two of each habitat type based on three or four electrofishing sweeps. *n*, total number of salmon caught per reach per season. Note that flats were within 100 m of numerous riffles and runs in the Catamaran Brook study area.



tions reflecting the heterogeneity of running waters (Hynes 1970; Hawkins et al. 1993). Boulder-strewn riffles, deep pools, beaver ponds, groundwater seeps, stream edges beneath shelf ice cover, off-channel backwaters, and woody debris jams are examples of some of the habitats used by stream fishes at different times during winter. Accessibility, as well as availability, to these various habitats are important factors in assessing survival of stream fauna because of the dynamic nature of the winter stream environment (Reimers 1963; Mackay 1979; Prowse and Gridley 1993) and increasing evidence of movement by stream fishes in winter (Chisholm et al. 1987; Cunjak and Randall 1993; Jakober 1995). Cunjak and Power (1986*a*) suggested that the continued activity by brook and brown trout in the Credit River system was adaptive because of periodic flooding, freezing, and thaws common to such temperate latitude streams. A similar explanation was originally used by Reimers (1963) to account for the winter feeding by rainbow trout in a Californian stream.

Instream variability and habitat shifts

Variability of instream conditions during winter occurs even within habitat types, or across the width of a river. In Idaho streams, Riehle and Griffith (1993) and Griffith and Smith (1993) have shown that, as water temperatures declined below 8°C, juvenile salmonids concealed themselves during the day primarily amongst boulders with low imbeddedness, vegetation, and undercut banks. In contrast, Cunjak (1988*a*) found that most juvenile Atlantic salmon sheltering beneath rocks in a Nova Scotian river during the day were closer to midstream than to stream margins. This difference might be explained by the interaction of fine sediments, ice, and associated water flow patterns. Although ice was rare in the Idaho study, shore ice was common in the Nova Scotian stream. Ice tends to deflect and concentrate water current (Prowse 1994*a*) toward midstream (thalweg), thereby minimizing substrate imbeddedness and sediment deposition, which was more likely beneath shore-bound ice along the stream margin. It is also possible that the salmon parr observed by Cunjak (1988*a*) during the day may have moved to stream margin microhabitats at night, when they emerge from beneath rock shelters. Heggenes et al. (1993) found juvenile brown trout in ice-covered Norwegian rivers at night, moving to the stream margins and other areas with low water velocities including streambank areas. Diel variation in preference, and modifications imposed by hydraulics and physical structure are, therefore, important when considering habitat use.

As indicated earlier, and suggested by others (Hartman 1965; Cunjak and Power 1986*a*; Heggenes et al. 1993; Pajak and Neves 1987; Chisholm et al. 1987; Swales et al. 1986; Nickelson et al. 1992*a*; Griffith and Smith 1993), winter habitat selection often differs from that in summer, generally involving movement to areas with lower water velocity (day and night) and suitable daytime cover. Where adequate wintering conditions are available nearby, the distance moved from summer rearing areas may be relatively short, simply to adjacent habitat types. In Wyoming streams, Chisholm et al. (1987) found that adult brook trout, radiotagged for two winters, moved an average of 86–163 m (mainly downstream) preferring low water velocity areas (i.e., <15 $cm \cdot s^{-1}$). Seasonal electrofishing surveys (summer and early winter) in different habitat types of two stream reaches in Catamaran Brook, New Brunswick (Fig. 3), demonstrated relatively greater use, by juvenile Atlantic salmon in winter, of flats (i.e., slow-flow habitats with gravel–rubble substrate). This was most obvious in the Middle Reach flats, which were deeper than those in the Lower Reach. Riffles and runs, which were preferred by salmon in summer, were used proportionally less than flats in early winter (Fig. 3).

River ice

During winters with low stream discharge but with an abundance of ice precluding access to adjacent stream habitat types, Cunjak and Randall (1993) suggested that instream movement (to more suitable habitats) was significantly restricted and contributed to substantial mortality. For their three study streams in eastern Canada, estimated mortality of resident juvenile Atlantic salmon over winter was 25–57%, being highest in the stream where winter conditions were most severe and in that year when ice and low streamflow could have restricted instream movement (Cunjak and Randall 1993). Subsequent research in a variety of habitat types in Catamaran Brook corroborated these estimates; winter mortality exceeded 65% of the resident salmonid population during that winter when streamflow was least and ice accumulation substantial (R.A.

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Cunjak, unpublished data). In British Columbia, Bustard (1986) estimated similar winter mortalities of 30–60% for juvenile salmonids in side-channel habitats exposed to severe freezing and suggested that the reduced streamflow and ice conditions of interior streams (Fig. 2) were the reason that many juvenile salmonids overwintered in mainstream habitats where suitable water depth was maintained. In coastal rivers, in contrast, winter is a period of high streamflow (Fig. 2) and juvenile salmonids often overwinter in side-channels, floodplain sloughs, and riverine ponds (Bustard and Narver 1975*a*; Cederholm and Scarlett 1982; Tschaplinski and Hartman 1983; Hartman and Brown 1987).

Chisholm et al. (1987) noted evidence of habitat exclusion by ice for brook trout overwintering in those stream sites (low elevation) where abundant surface ice occurred in the riffles. In contrast, Berg (1994) found little evidence of habitat exclusion (based on a minimum 6 cm depth criterion beneath ice) for rainbow trout in ice-covered pools along an elevational gradient in California's Sierra Nevada during two relatively dry winters. Berg did note limitations in trying to apply his results to geomorphically different streams, particularly wide, shallow, low-gradient streams where ice would more likely limit trout movements. Cunjak and Caissie (1994) suggested that frazil ice accumulations in large river pools (see above) may preclude their use for overwintering Atlantic salmon kelts.

One of the many challenges facing fish biologists and resource managers is to appreciate (quantify) the significance of environmental variability and the subsequent biotic responses. Ice (surface, frazil, and anchor ice) is common in many North American rivers (Brown et al. 1953; Chacho et al. 1986; Brown 1994; White 1994) including the Great Lakes Basin (Barnes 1928; Benson 1955). Ice accumulation in pools can reduce winter habitat space (Fig. 4) and suitability. The environmental aspects of river ice has begun to receive some attention (Prowse and Gridley 1993; Berg 1994; Prowse 1994*a*, 1994*b*; Scrimgeour et al. 1994). How ice and its consequent influence on stream hydraulics may impact fish habitat, particularly the dynamics surrounding freeze-up and break-up events (Prowse 1994*a*), is still a mystery. Calkins (1989) in reviewing the winter habits of four stream salmonids, noted that no fisheries article that he reviewed had calculated the hydraulic properties or flow regime beneath ice cover. Such omissions need to be corrected to quantify availability and suitability of wetted space (habitat) beneath ice cover and how these usable areas change with different ice and streamflow regimes.

Backwater habitats and beaver ponds

Pool-like habitats and backwaters, because of the deep water and low-velocity conditions that they offer, are the winter habitat of choice for many stream fishes. Such conditions are also available in beaver ponds. That large, deep pools are often the habitat type in least supply in many small streams of today (e.g., Sedell and Luchessa 1982; Cunjak et al. 1993) is further evidence of the potential importance of beaver ponds as winter habitat. In Wyoming, Chisholm et al. (1987) found brook trout moving into a beaver pond in October where they remained active all winter. In Rocky Mountain streams, as autumn water temperatures declined below 7°C, densities of bull trout (*Salvelinus malma*) and cutthroat trout declined in all habitat types except beaver ponds where large aggregations of both species overwintered (Jakober 1995). The use of beaver ponds for overwintering was also noted for juvenile coho salmon in coastal Oregon streams (Nickelson et al. 1992*a*) and for coho salmon and Dolly Varden (*Salvelinus malma*) in a southeastern Alaskan stream (Chichagof Island) where survival was considered better relative to other winter stream habitats (A. Dolloff, U.S. Forest Service, Blacksburg, personal communication) although predation by otters was concentrated here in early spring (Dolloff 1993). In a beaver pond in Catamaran Brook, an aggregation of more than 60 brook trout (12–25 cm fork length) was observed (mid-October, water < 8°C), more trout than observed in any other pool in the system in the previous 3 years (R.A. Cunjak, unpublished data). In such shallow streams where ice cover is often in contact with the stream bed, a beaver pond may represent one of the few available wintering sites.

The value of beaver ponds as wintering habitats for fishes is underappreciated. The deeper water in the pond, and in the adjacent flooded backwaters, provide the requisite space where fish can aggregate and swim, even beneath a complete ice cover. Indeed, the frequency of occurrence of large winter aggregations noted in the above-cited research and in other winter studies (e.g., Hartman 1965; Bustard and Narver 1975*a*; Craig 1978; Paragamian 1981; Cunjak and Power 1986*a*) may be evidence that adequate winter habitat is limiting in many systems. Aggregations, therefore, may be useful as indicators of important wintering areas.

Large-scale habitat considerations

Movement to wintering habitats can involve long distances. In the North Ram River, Alberta, Brown (1994) found that radiotagged, adult cutthroat trout moved upstream and downstream an average of 1–2.4 km, but some moved as far as 7.6 km from the site of release to wintering pools. Apparently these movements were in response to changing subsurface ice conditions in the river, as trout sought suitable pools or "warm" groundwater inputs (Brown et al. 1994). Clapp et al. (1990) found that large (43.7–63.5 cm) brown trout in a Michigan stream had separate summer and winter ranges, with some fish moving approximately 10 km upstream to overwinter in slower, deeper parts of the river. Similar long-range movements were noted in the northwestern Miramichi River, New Brunswick, where some post-spawned Atlantic salmon (kelts) moved 5–10 km downstream to the head of tide (R.A. Cunjak, unpublished data). As in Alberta, kelt movement was likely in response to frazil ice accumulation in the riverine pools (e.g., Cunjak and Caissie 1994); such accumulations were minimal in tidal water because of the flushing action of the tides. Adult largemouth bass in the upper Mississippi River were active in winter, moving 3–14 km to wintering areas (slightly warmer, no-flow backwaters), which may be the limiting habitat for centrarchids (largemouth bass, bluegills, and crappies) in this part of the Mississippi (J. Pitlo, personal communication). In some ice-covered northern Ontario rivers, adult lake sturgeon (*Acipenser fulvescens*) equipped with physiological radiotags (to monitor electromyogram activity) moved at a rate of ≈6 km·day^{-1} to overwinter in a deep pool at the confluence of two rivers, where they remained active until the start of the spawning migration in mid-January (S. McKinley, University of Waterloo, Waterloo, Ont., personal communication). In the

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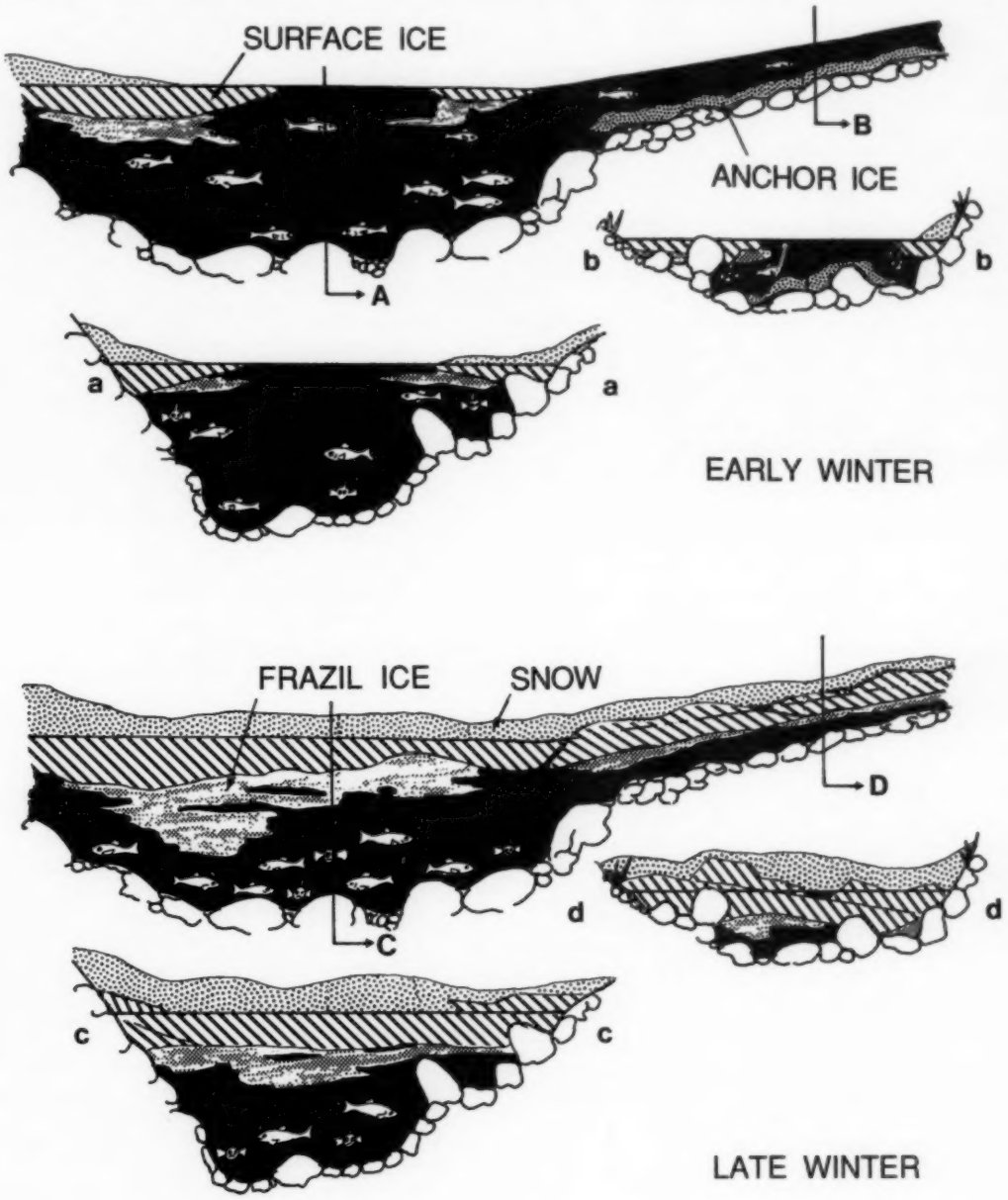
Fig. 4. Conceptual representation of the change in habitat availability in a temperate stream riffle and pool as winter progresses and ice accumulates. Open sections in riffles may generate anchor ice and frazil ice, which can subsequently restrict habitat available to fish in downstream stream sections and may contribute to ice dam formation and streamflow alteration (modified from Power et al. 1993).



arctic, where winter conditions can be severe and suitable winter habitat is least available, migration distances between summer and winter areas can be ≈100 km (West et al. 1992). These long-distance movements between summer and winter areas emphasize the need for a seasonal appreciation of habitat requirements and a large-scale river basin approach to fisheries management (Clapp et al. 1990).

Such long-distance winter movements are in marked contrast to some published research on instream movements. For example, Garcia deLeaniz (1989) found that home areas were less than 8 m^2 for 75% of the marked Atlantic salmon parr that were monitored for 17 months in a Scottish stream. Heggenes et al. (1991) found limited movement by cutthroat trout between January and August in a British Columbia stream where

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63.2% of the recaptured individuals moved less than 10 m. In these latter two studies, the absence (British Columbia) or minimal amount of ice (Scotland) in the streams (which could influence winter habitat suitability) may partly explain the differences in movement. Alternatively, where suitable winter habitat is immediately available, and relatively stable throughout the winter, long-distance movement is unnecessary (Bjornn 1971; Dolloff 1987).

The preceding should impress upon habitat managers that river systems must accommodate the range of movement and habitats used by stream fishes in winter. Further, protection of preferred winter habitat(s) is only one consideration for habitat conservation. Just as important are the "corridors," the stream channels that permit access between seasonal habitats. Some fishes move many kilometres to overwinter in relatively few suitable habitats, and many continue to move among different habitats during the course of the winter. Therefore, winter habitats need to be viewed not as discrete units but rather as a dynamic continuum within a population's distributional range. Such a scenario is admittedly daunting in trying to establish guidelines for habitat conservation. The task becomes further complicated when considering the potential impacts to winter environments from anthropogenic activity in stream basins.

Impacts to winter habitat from land-use activity

Fisheries managers today need to understand and quantify how land-use activity in a stream basin might alter habitat. Ideally, before attempting such a cause–effect linkage, one needs first to understand the natural variability within the stream before attempting to assess man-made impacts (Rinne 1990). This is a difficult ideal to attain because of our limited knowledge of stream conditions and species' habitat requirements in winter. Nevertheless, some general considerations and associations are possible to assist management decisions relating to winter habitat impacts.

Loss of habitat complexity

For those fishes that prefer to overwinter beneath medium to large substrate (i.e., cobble–boulders), habitat quality and availability is deleteriously affected by land-use activity that introduces fines into the stream, thereby imbedding potential winter cover. Simulating winter cover conditions in a small stream, Bustard and Narver (1975*b*) demonstrated that juvenile salmonids prefer clean rubble over silted rubble, and the preference was strongest at the lowest water temperatures (i.e., 2–6°C). Winter electrofishing by Griffith and Smith (1993) in portions of the Snake River, Idaho, indicated that boulder sites that were heavily imbedded (25–50% fines) had <30% of the cutthroat trout density of adjacent boulder sites that were moderately or slightly imbedded (<25% fines). In a Nova Scotian river subject to erosion and sedimentation from land-use activity in the catchment, Cunjak (1988*a*) found that 40% of the salmon parr that he observed underwater in winter were located beneath stones in salmon redds, which accounted for only 10% of the study area. He suggested that this disproportionate use of redds for overwintering was a function of high imbeddedness in the stream.

Improper forestry and agricultural activities can introduce fine sediment to streams, especially where suitable riparian buffer strips are inadequate to prevent erosion and soil runoff (Brown and Krygier 1971; Barton and Taylor 1981; Campbell and Doeg 1989; Hartman and Scrivener 1990). In Prince Edward Island streams, sedimentation from the erosion of agricultural land is a serious problem for aquatic habitats. Recently, 253–305 t(1t = 1000 kg) of topsoil was excavated from a pit at the base of a 12.2-ha potato field in the West River catchment, in midsummer; after three strong rain events (≈6 weeks), the pit completely filled in with eroded soil, which then overflowed into the river (T. Dupuis, Atlantic Salmon Federation, Charlottetown, P.E.I., personal communication). Similar problems are realized in the sand-plain streams of Norfolk County along the north shore of Lake Erie (personal observation), which resemble Prince Edward Island in geology, topography, and land use. After forestry activity in the Alsea catchment (Oregon), yields of suspended sediments increased from 26–97 to 90–300 $t \cdot km^{-2} \cdot year^{-1}$ (Beschta 1978, as cited in Hartman and Scrivener 1990). In Carnation Creek, British Columbia, where the most detailed study of fishery–forestry interactions has taken place, deposition of fines increased 4.6–5.7% following logging coincident with a decline in survival to emergence for coho and chum salmon (Scrivener and Brownlee 1989). Winter habitats of most stream fauna (e.g., Campbell and Doeg 1989; Cobb and Flannagan 1990), not only fishes, are deleteriously affected by such sediment loading.

Pools, side-channels, backwaters, large organic debris (LOD) complexes, and some undercut stream margins provide important low water velocity refugia and instream cover, conditions preferred by many stream fishes in winter (see above). However, the nature of these habitats often predisposes them to infilling and damage from improper land-use activities, thereby reducing their suitability as winter habitat (e.g., Bustard and Narver 1975*b*; Tschaplinski and Hartman 1983; Hartman and Brown 1987; Hillman et al. 1987). For example, backwater habitats along the upper Mississippi River act as thermal (and flow) refugia during winter for many centrarchid fishes and are infilling at an average rate of 2.5–6.3 $cm \cdot year^{-1}$ (J. Pitlo, DNR, Bellevue, Iowa, personal communication). Sedimentation is one of the major causes of habitat degradation of these backwater refugia (Brietenbach and Peterson 1980, cited in Pitlo 1993) by reducing water depth and oxygen content. Consequently, Pitlo (1993) suggested that winter habitat may be the limiting habitat for many centrarchids of the Upper Mississippi River. Tschaplinski and Hartman (1983) found that juvenile coho populations were better able to resist displacement from autumn-winter flood events in Carnation Creek if instream cover (LOD) remained in the winter habitats (i.e., pools). In those stream sections adjacent to clearcuts, LOD was scarce and coho populations were reduced by 63–74%; in comparison, a section with stream-side buffer strips retained LOD and coho reductions were only 40–45%. Heifetz et al. (1986) estimated that 73% of pools (the preferred winter habitat of juvenile salmonids in Alaskan streams) were formed by LOD and that stream reaches in clearcuts without buffer strips had significantly less area of pool habitat. Loss of stream habitat complexity is common to river catchments where improper land use has occurred.

Alteration of streamflow

Winter streamflow contributes a proportionally smaller

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amount to the annual hydrograph as one moves away from the moderating influence of a coastal climate to the continental interior (Fig. 2), where winter precipitation is more likely to fall as snow and where freezing conditions prevail. Therefore, the potential impacts to fish habitat from waterflow alteration need to be viewed in the context of the local hydrologic regime. Hydroelectric facilities divert, store, and release water for generating energy largely in response to human demands for power rather than with consideration to natural streamflow patterns. Proposals for water withdrawal from streams during winter for snowmaking for alpine ski operations are increasing in New England (R.A. Cunjak, personal observation) and probably elsewhere. Withdrawals effectively remove a portion of the streamflow with no return until late winter or spring when a larger than normal snowpack melts. Regulation of streamflow, be it for hydroelectricity or for other purposes, can markedly change the natural discharge pattern (Fig. 2) and the seasonal cues to which the resident stream fauna have evolved specific strategies. For example, the suppression of major flood periods in regulated West Coast streams might preclude access to floodplain winter habitats for juvenile salmonids or their return to the main channel in spring.

Barriers to instream migration can deny access to wintering areas. As noted previously, some stream fishes (e.g., salmonids, centrarchids, sturgeon) move long distances prior to and during winter. How well fish can locate alternative wintering areas once dams are built is unknown. The impacts will be deleterious where winter habitats are limited in abundance and where fish demonstrate strong site fidelity for particular wintering areas. Pitlo (1993) found evidence of homing to specific wintering sites in the Upper Mississippi River; several radiotagged largemouth bass were found in the same general area in summer but moved more than 5 km to widely separated backwater habitats in winter, bypassing backwaters used by other wintering bass.

Water withdrawal and its direct influence on reducing available habitat (wetted space) probably impacts stream fish populations more than any other winter alteration of streams. The situation is most pronounced in shallow streams and rivers (often the most productive rearing habitats for juvenile salmonids) and is exacerbated by ice conditions (Power et al. 1993). West et al. (1992) noted the susceptibility of Alaskan grayling to habitat damage from water abstraction (for construction of ice roads, airstrips) because of the shallowness of rivers and the extremely limited winter habitat (i.e., unfrozen water beneath ice). Griffith and Smith (1995) noted that when winter discharge was kept low in a regulated stream, juvenile rainbow trout could not use near-bank concealment habitat that had held a high density of fish throughout a previous winter. Chisholm et al. (1987) suggested that the impact of winter water withdrawal may be more severe at low-elevation sites because of habitat exclusion by surface and subsurface ice accumulation and "... the lack of suitable means for determining winter streamflow needs under these conditions."

A winter reduction in streamflow will generally accelerate ice formation. Land-use activities such as forestry and agriculture often result in wider, shallower stream channels, which in turn are conducive to greater ice accumulation. Together, these effects can markedly reduce available habitat beneath ice cover in rivers. Maciolek and Needham (1952) reported on the mortality of brown and rainbow trout in Convict Creek, California, when subsurface ice accumulation precluded water flow into side-channels where trout were subsequently stranded. Barns (1987[1]) in his report on potential impacts of hydroelectric development in the Nechako River, British Columbia, suggested that the reduced intragravel flow to chinook salmon redds would affect incubation time, development, and survival of eggs and alevins. Curry et al. (1992) cautioned that streamflow reductions for hydroelectric development in the Nipigon River, Ontario, could alter groundwater flow to brook trout incubation habitat and result in freezing of eggs and alevins.

The reduction in accumulated thermal units as a consequence of water withdrawal could severely impact fishes that are poorly adapted for activity at freezing temperatures. The discovery of moribund and dead fish (representing 37 species) in the upper Mississippi River was attributed to their inability to cope with water temperatures below 1°C in the main channel and because warmer off-channel refugia (backwaters) were lacking nearby (Bodensteiner and Lewis 1994), possibly because these habitats had been altered by land-use activity in the catchment (see Pitlo 1993). Similar impacts might be expected for fishes that are near the northern limit of their distributional range. In the Great Lakes drainage, species such as white perch (*Morone americana*), which have a low tolerance for near-freezing winter temperatures (Johnson and Evans 1991), would likely be deleteriously affected by activities that resulted in lower water temperatures.

Stream enhancement and winter habitat

In some cases, attempts at "enhancing" stream habitats in summer may have negative consequences for wintering fish. That is, summer gains in production may be nullified by constraints related to winter carrying capacity. Streamside debris–brush removal, particularly of alders, is a popular component of some stream enhancement projects (e.g., OMNR 1986). Improved access (for anglers), increased streamflow, and flushing of fines are often cited to rationalize the habitat alteration. Such changes were made along a section of the Valleyfield River, Prince Edward Island, where stream enhancement was carried out in 1988–1989 (R.A. Cunjak, unpublished data). Alders, still present in a control area upstream, impeded water movement and resulted in the littoral deposition of fines and the formation of a wide channel with shallow stream margins. In the treatment zone, in contrast, alder removal led to faster streamflow through a narrower channel with little depositional area. A seasonal snorkeling census of brook trout abundance in both areas indicated that fewer trout used midstream or margin habitats post-treatment in comparison with the control (Fig. 5). Habitat alteration in the treatment area scoured midstream macrophytes where brook trout often sought cover and eliminated the shallow (<10 cm depth), low-flow, alder margins, which young-of-the-year trout used extensively, particularly in winter. Some trout were able to find suitable habitat in proximity to a few enhancement structures (i.e., deflectors and low-head barriers) placed nearby, but these conditions favoured mainly older trout (R.A. Cunjak, unpublished data).

[1] Barns, R. 1987. "Expert" report. Prepared for court case on environmental assessment of proposed Nechako River hydroelectric project (ALCAN).

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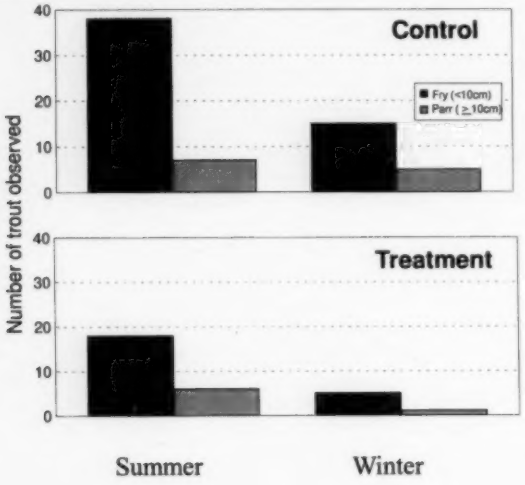
Fig. 5. Mean number of brook trout observed during underwater observations in two stream reaches of the Valleyfield River, Prince Edward Island, in summer (June–September 1989) and winter (December 1989–March 1990). Both sites were of similar width and length. The treatment site underwent bank-side brush (alder) removal and the installation of stream enhancement structures in 1988; no such changes occurred within the control reach, which was just upstream of the treatment.



Ruggles (1966) carried out comparative experiments in stream channels to increase smolt production of juvenile coho salmon by increasing winter cover (cement blocks). Contrary to expectations, smolt production was markedly higher in channels without cover. In a small stream on Vancouver Island, Mason (1976) attempted to increase winter habitat for juvenile coho salmon by constructing streamside refugia. However, less than 5% of the introduced coho used the refugia as most fish remained in the natural stream habitats and eventually emigrated during winter freshets. Mason indicated that "a 6- to 7-fold increase in potential smolt yield induced by a supplemental feeding strategy during the summer was nullified by the natural carrying capacity of the stream over winter." Constructed pool habitat (plunge pools and dammed pools) in Oregon streams, which were effective in providing suitable summer habitat for juvenile coho salmon, were used significantly less in winter (Nickelson et al. 1992*b*) when coho preferred alcove (off-channel) habitats (Nickelson et al. 1992*a*). Cunjak and Power (1987) studied winter cover use by brook and brown trout in a small spring-fed tributary of the Credit River by comparing frequency of use of submerged versus above-water cover, in riffle and pool habitats. Both species preferred submerged cover, but brown trout frequented only the pool habitat closest to the stream mouth, whereas brook trout used submerged cover with similar frequency in all four habitat types. The use of riffle habitats in winter was in contrast to where brook trout normally were observed in other Credit River sites (Cunjak and Power 1986*a*) and was explained by the relatively low focal point velocities beneath riffle cover structures caused by accumulation of debris behind which trout frequently positioned themselves (Cunjak and Power 1987). Obviously, these results underline the complexity of winter habitat requirements of stream fishes and our relative ignorance of what constitutes important habitat in winter and summer.

More consideration needs to be given to the efficacy of habitat enhancement projects in winter. Calkins et al. (1989) found that frazil and anchor ice often accumulated around boulders and deflectors and eventually formed a surface ice sheet. Despite a relatively mild ice break-up in the year of study, a 70-kg boulder was displaced by ice floes and led the authors to recommend that boulders be at least 100 kg for use in such projects. Boulders, which act as cold sinks, also play a major role in the initial freeze-up process (Calkins and Brockett 1988). Where partially exposed above the water, boulders formed air gaps when surface ice perched on them as water levels dropped (Calkins et al. 1989). Sub-ice air gaps can be ecologically significant by inhibiting further ice growth and acting as an insulating layer, an interface for aeration, an "exit" for winter-emerging macroinvertebrates, and a corridor for sub-ice movements by fish-eating mammals (Calkins et al. 1989).

Modeling habitat conditions in winter

Habitat simulation models and instream flow methodologies are commonly applied throughout North America (Reiser et al. 1989), often with the objective of assisting biologists and managers in providing adequate habitat protection for aquatic resources subject to proposed streamflow alteration (Shirvell 1989; Armour and Taylor 1991). Most of the habitat-suitability curves used in these models are derived from measurements made during spring–autumn and are not appropriate for winter habitat simulations. In two Virginia streams, Pajak and Neves (1987) found that rock bass (*Ambloplites rupestris*) distribution was most restricted in winter (in deep pools) and led the authors to suggest that winter conditions were probably more appropriate than summer low flows in determining habitat suitability for these populations.

Previously cited evidence of shifts in seasonal habitat preferences of stream fishes and the unique hydrologic characteristics of an ice-covered stream in winter (e.g., Calkins and Brockett 1988; Calkins 1989; Prowse and Gridley 1993; Prowse 1994*a*), which the hydraulic submodel of PHABSIM cannot properly simulate, should dissuade the use of these instream flow models in winter until more appropriate simulations and validations are carried out (e.g., Berg 1994; Martinson et al. 1994). Similar concerns regarding the use of these models for simulating conditions in ice-covered rivers were made by Petryk et al. (1994). Indeed, surveys of state and federal agencies concerning instream flow practices in North America (Reiser et al. 1989) found that a number of respondents identified the need to develop new methods for determining winter flow requirements of fishes.

Conclusions

Stream fishes have adopted many adaptive mechanisms to meet the demands of winter. The complexity and dynamic nature of a stream in winter must be viewed from a spatial, as well as a temporal, aspect. That is, winter habitat suitability can, depending on individual preferences and local environmental conditions, be achieved in any number of habitat types,

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stream reaches, and basins. Further, habitat suitability and use can vary with time over the course of winter (e.g., early winter vs. late winter vs. midwinter; day vs. night). Such complexity suggests a fragility in the inter-relations between animal and habitat in winter. The frequency and prevalence of significant winter mortalities seem to emphasize this fragility.

Assurance of winter habitat protection for the many life stages and species that comprise a fish community will not be an easy task for fisheries managers. Because of the variety of winter habitat preferences and the long distances that some fishes travel between summer and winter sites, the most obvious advice is to maintain habitat complexity. In the case of degraded streams, winter habitat enhancement needs to restore complexity. That each stream is different and unique is known to any field biologist but an unwelcome statement to a manager trying to develop habitat guidelines with broad geographic applicability. However, there are some generic rules regarding winter habitat that apply to all streams. These rules include the understanding that diverse, complex microhabitats and the corridors that allow access between them are essential for overwintering fishes, that summer and winter habitat requirements may be different, that groundwater discharge zones provide winter refugia, that ice can markedly influence habitat suitability, and that land-use activities that increase sediment loading and reduce streamflow can deleteriously alter availability of winter habitat. Quantitative data demonstrating the importance of winter habitats, and contrasting survival under different winter conditions, are largely lacking and can only be obtained by applying the type of effort previously reserved for the spring–autumn period. Not until we consider winter as part of the field season rather than a time to work up summer data, will we be able to effectively conserve and manage fish habitat.

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Long-term enhancement of habitat for salmonids in acidified running waters

Gilles L. Lacroix

Abstract: Application of crushed limestone on the bed of an acidic brook enhanced Atlantic salmon (*Salmo salar*) spawning habitat, and the mitigation strategy resulted in improvements in the survival of juvenile Atlantic salmon and brook trout (*Salvelinus fontinalis*). There was a small, lasting increase in pH in the limed section of the brook and downstream over 8 yr. Limestone was replenished once after 4 yr because of washouts during floods; otherwise, requirements for maintenance were low. After liming, Atlantic salmon consistently dug most redds in the limed section, but this preference was possibly related to physical enhancement of spawning areas rather than to high pH. Liming resulted in a twofold increase in the number of occasions where more than a few juvenile Atlantic salmon survived severe acidic episodes in the brook. Brook trout were tolerant of lower pH episodes than juvenile salmon but, like salmon, they also responded to changes in minimum pH as a result of liming. Densities of age–0 salmon and brook trout were related to seasonal and interannual variability in pH, but they were always greater in the limed section than in the unlimed, control section upstream, especially at times when the difference in pH between sections was the largest.

Résumé : L'application de calcaire concassé dans le lit d'un ruisseau acide a amélioré l'habitat de reproduction du saumon atlantique (*Salmo salar*), et la stratégie de compensation a fait beaucoup pour la survie des juvéniles du saumon atlantique et de l'omble de fontaine (*Salvelinus fontinalis*). On a constaté une augmentation légère mais durable du pH dans la section chaulée du ruisseau ainsi qu'en aval pendant huit ans. Il a fallu rajouter du calcaire une fois après quatre ans pour reconstituer celui qui avait été entraîné par les crues; ceci mis à part, les besoins d'entretien ont été minimes. Après le chaulage, le saumon atlantique a régulièrement creusé la plupart de ses nids de fraye dans la section chaulée, mais cette préférence dépendait peut-être plus de l'amélioration physique des frayères que du pH élevé. Le chaulage a multiplié par deux les cas où un nombre non négligeable de saumons atlantiques juvéniles ont survécu à de graves épisodes d'acidité dans le ruisseau. L'omble de fontaine a mieux toléré les épisodes de pH plus faible que le saumon juvénile, mais comme le saumon, il a également réagi aux changements du seuil minimal de pH apportés par le chaulage. La densité du saumon et de l'omble de fontaine d'âge zéro était tributaire de la variabilité saisonnière et interranuelle du pH, mais elle était toujours plus forte dans la section chaulée que dans la section témoin non chaulée située en amont, surtout aux moments où la différence de pH entre les sections était la plus grande.
[Traduit par la Rédaction]

Introduction

Application of limestone gravel to the bed of a small acidified brook was used by Lacroix (1992) to mitigate low pH in an attempt to enhance habitat for Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*). The method was selected to inexpensively provide a better environment for eggs, alevins, and fry and to limit the periods of lethal pH for juvenile salmon and brook trout in a section of the brook. The purpose was to assess the immediate and long-term effectiveness of the methodology to alter water chemistry and to have a beneficial impact on fish. The intent in liming was not to maintain pH at circumneutral levels at all times but rather to increase pH slightly and maintain it above low lethal levels during acidic episodes while retaining the seasonal variability. Such changes would be in line with the type and magnitude of changes in pH possible over eastern Canada during the next several decades as a result of the control of SO_2 emissions (Clair et al. 1995). Therefore, the situation created by liming in the brook also allowed for an assessment of the potential for recovery of Atlantic salmon in acidified waters in response to less severe conditions (i.e., a small increase in pH) during annual acidic episodes.

An impact study is best designed when it judges impact effects against previously collected baseline data (Green 1979). Control in both space and time are, therefore, prerequisites of an optimal impact study design, but monitoring studies often end up having to proceed without one or the other. In this case, operational requirements and demands indicated an urgent need for testing some inexpensive liming methods in small acidified brooks of Nova Scotia. This prevented long-term study of a brook before the "impact" (i.e., liming) to provide a control period for assessing effects. However, Fifteen Mile Brook was selected because some baseline water chemistry and biological information were available from studies conducted before liming. Lacroix (1985) previously estimated the survival of eggs and alevins of salmon in relation to the chemistry of interstitial water in redds in the brook. Lacroix et al. (1990) also measured the physiological responses of brook trout in the brook during episodes of low pH. As an alternative to a temporal control of long duration, limestone was only applied to a short section of the brook and a similar section immediately upstream was left undisturbed to

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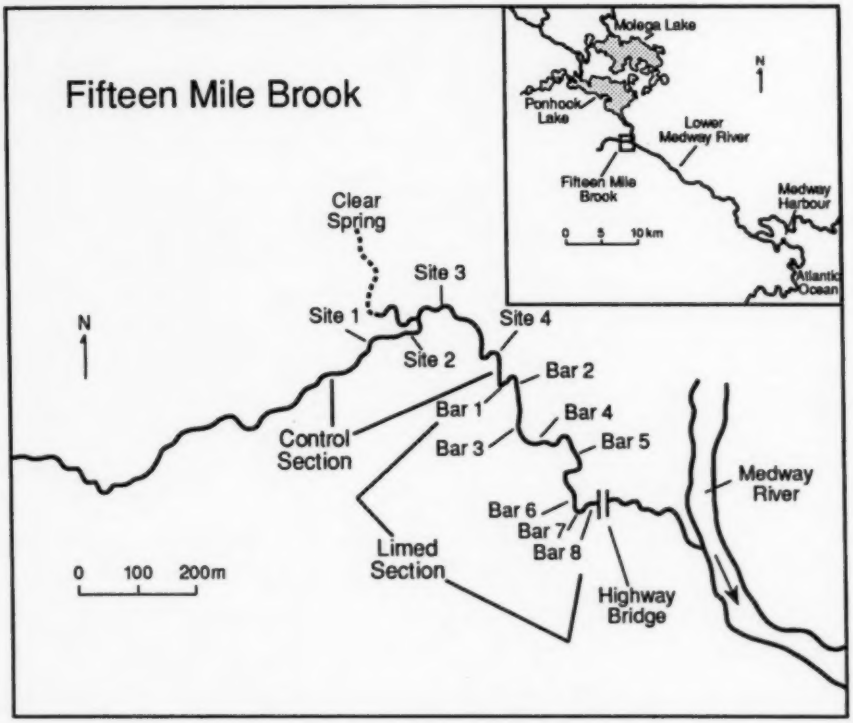
Fig. 1. Maps of Fifteen Mile Brook and the lower Medway River (inset) showing the location of control and limed sections, limestone bars, and sites of water sampling.



provide a control in space and a means of inferring the impact of liming.

The liming method tested was chosen because it was relatively inexpensive, application was easy, and it was hoped that maintenance would be low. However, it had received little or no evaluation of impact and effectiveness over time (Pearson and McDonnell 1975; Keller and Gunn 1982; Watt et al. 1984). An evaluation of the degree of maintenance required by this method of liming and the extent, both spatial and temporal, of its effectiveness to mitigate low pH was, therefore, one of the goals of the study. The assumption tested was that it required little or no maintenance and could provide a lasting effectiveness.

The study was conducted to test that liming resulted in significant changes in water chemistry and in the populations of Atlantic salmon and brook trout against the null hypothesis of no change. An initial assessment of the effects of liming, based on short-term (i.e., 3 yr) monitoring, indicated that the resulting small increases in pH could be leading to a recovery of the Atlantic salmon population (Lacroix 1992). This study is an extension of the chemical and biological monitoring in control and limed sections of the brook to provide a long-term assessment of impacts and changes. It spans 8 yr during which limestone had to be applied a second time to replenish some areas after severe washouts during floods. The consequence of further collection of data on the conclusions of Lacroix (1992) and the value of streambed liming to enhance habitat for fish in acidified running waters were examined. The limitations of the study design in relation to capability to detect a change, the nature of the change, and the degree of impact associated with liming were also examined.

Methods

Description of study area and habitat

Fifteen Mile Brook was a small, second-order stream entering the mainstem of the Medway River in the lower reaches of the watershed, downstream of Ponhook Lake (Fig. 1). The stream was crossed near its mouth by the cement bridge of a secondary highway. It had an overhanging forest canopy providing cover over most of its length, except along several bog areas in its middle reaches. The forest along the lower reaches where the study sites were located was composed primarily of mature pine immediately along its bank. Water in the brook was brown and dominated by organic acids because of these bog areas in the drainage and the type of cover. There was a first-order, comparatively clear, spring-fed brook entering the lower reaches. The brook received little direct human impact. There were no habitations immediately along the brook other than two rarely used camps, one near the middle bog area and the other at the mouth.

The stream in the lower reaches where the study area was located was meandering, composed of pools, riffles, and runs with an average width of 4.8 m. The upstream boundary of the control, unlimed section was established at the upstream limit of spawning by salmon in the brook based on a previous survey (Lacroix 1985). The control section extended, from a pool at the upstream end, about 300 m downstream to the first bar where limestone was applied. The limed section then extended about 300 m from the upstream end of the first limed bar to the last pool in the brook immediately downstream of the final

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Table 1. Available habitat (means followed by SD and *n* in parentheses) in control and limed sections of Fifteen Mile Brook.

	Control section		Limed section	
Water depth (cm)	10.0	(9.4, 372)	15.9*	(13.6, 514)
Average water velocity ($cm \cdot s^{-1}$)	8.4	(9.6, 372)	11.6*	(11.9, 514)
Bottom water velocity ($cm \cdot s^{-1}$)†	6.7	(8.9, 372)	8.9*	(10.7, 514)
Bed material grain size (mm)	79	(52, 2499)	60*	(38, 2250)

*Significant differences between sections (*t*-test, $P < 0.005$).
†Water velocity measured 2 cm above the streambed.

limed bar. From there, the brook ran another 200 m to the mouth, most of which was on ledges of exposed bedrock with no suitable spawning or nursery habitat. This last reach was, therefore, excluded from the study area.

Available habitat in each section of the brook was characterized by measuring water depth, average water column velocity, bottom water velocity, and bed surface material grain size along established transects as described by Lacroix et al. (1995). The brook was mostly shallow (Table 1). Pools rarely exceeded 1.5 m deep, but many had large fallen trees and undercut banks that could provide cover for fishes. The streambed material was mainly gravel, 50% finer (by number) than 65 mm, and it had excellent permeability (Lacroix 1985). The limed section was deeper, had higher mean and bottom water velocities, and finer bed material than the control section upstream (Table 1). Coefficients of variability were 86–94% for depth, 103–114% for average water velocity, 120–133% for bottom water velocity, and 63–66% for bed material. Thus, habitat available in each section was sufficiently varied that parameters were within ranges suitable for the different age-classes of juvenile Atlantic salmon and brook trout (Lacroix et al. 1995).

Other than Atlantic salmon and brook trout, American eel (*Anguilla rostrata*) could always be found in both sections of the brook; they were most abundant in the summer and were usually rare in autumn (Lacroix 1992). Other species found infrequently in the brook included white sucker (*Catostomus commersoni*), brown bullhead (*Ictalurus nebulosus*), and threespine stickleback (*Gasterosteus aculeatus*).

Application of limestone

Approximately 200 t of crushed (4-cm grade) dolomitic limestone were added to the bed of Fifteen Mile Brook on 12 and 13 September 1987 to increase pH (Mayhew 1989; Lacroix 1992). The limestone was applied in the lower reaches, 250–525 m from the mouth of the brook. It was distributed over eight separate areas in that section using light machinery to form eight bars 30–50 cm deep across the brook. The limestone was moved with a small front-end loader, with a 2-m^3 bucket, to the desired location for application using several entry points along the stream. The machinery was driven along exposed sections of streambed at a time of extremely low water flow. After dumping, the limestone was spread and leveled by dragging the bucket in an upstream direction.

The limestone bars were positioned at the downstream end of pools and at the head of riffles or in runs and shaped to simulate the preferred spawning habitat for salmonids. The bars were also manually shaped to create minimal disturbance to channel characteristics, water depth, and stream flow routing. The depth of crushed limestone was limited to ensure that the bars did not impede the movements of fish. Throughout the procedure, care was taken to avoid pools and to minimize disturbances in the stream, to stream banks, and to habitat adjacent to the limed areas.

The amount of limestone initially added to form each bar ranged from 7.5 to 15 m^3 (16.7–33.5 t). An additional 100 t of limestone were added on 7 November 1991 to replenish four of the eight bars (numbers 1, 3, 4, and 6, from upstream to downstream) with about the same quantity as that applied initially. This second application was made to maintain the amount of limestone on these bars where it had washed away after severe floods in the spring of 1990 and 1991. The total amount of limestone was not increased over the initial amount added because the mitigative strategy was to attempt to maintain the initial pH difference achieved rather than to see how much it could be increased. This strategy also issued from the initial objective of assessing the long-term response of fish to a small increase in pH in an acidified brook.

Monitoring of water chemistry

Water was collected in Fifteen Mile Brook in the control section immediately upstream of the limed section (i.e., at site 4) and in the limed section downstream of bar number 8 (Fig. 1). Starting in August 1987, samples were taken at 1- or 2-week intervals until 1990 and then about monthly until December 1994. Water discharge was estimated for each sampling occasion as described by Lacroix (1992). Water temperature was also recorded on each occasion. Water samples were analyzed using standard methods as described by Lacroix and Kan (1986) and Lacroix (1992) and the following parameters were regularly determined: pH, acid neutralizing capacity (ANC), Na, K, Ca, Mg, Cl, SO_4, dissolved organic carbon (DOC), total dissolved Al, exchangeable Al, and extractable Fe and Mn. Several other parameters, SiO_2, F, Cd, Cu, Pb, and Zn, were determined less frequently.

Before liming, pH was measured at about 100-m intervals along the study area in August 1987. Then, after liming, pH was measured on 11 occasions before acidic episodes and on 13 occasions after acidic episodes at 4 sites along the control section, in the small spring where it enters the brook in the control section, downstream of each of the 8 limestone bars in the limed section, at the mouth of the brook, and in the Medway River (Fig. 1). This was done to obtain details on the changes in pH that occurred along the control and limed sections under a variety of conditions.

Monitoring of fish populations

Before liming, estimates of density for all fishes in Fifteen Mile Brook were made by electrofishing in October 1986 at one site (later to be limed), and in August 1987 at four sites (i.e., two contiguous sites in the section to be limed and two contiguous sites in the control section, with a 75-m area left unfished between sections). After liming, the density of fishes was estimated in the control section and in the limed section of the brook twice annually, in August and October, from October 1987 to October 1994. In 1991, density was estimated only once in October. In October 1987 (i.e., 1 month after liming), the same four sites as in August 1987 were fished. Thereafter, two of these sites, one in each section, were fished.

Fish density was estimated separately by species and age-class using the sequential-removal method (i.e., Zippin with maximum likelihood solution) as described by Lacroix (1989*a*). Sites, enclosed by barrier nets, were electrofished, and at least four catches were made to calculate density. The areas fished included several pools and riffles and were about 500–700 m^2, depending upon stage height.

In 1987, all juvenile Atlantic salmon and brook trout captured by

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Table 2. Mean pH (with SD given in parentheses) along control and limed sections of Fifteen Mile Brook before and after acidic episodes between September 1987 and December 1994 (pre-episode $n = 11$; post-episode $n = 13$).

Site description	Distance from river mouth (m)	Mean pH			
		Pre-episode		Post-episode	
Control section					
Site 1	800	5.06*a*[§]	(0.44)	4.44*a*[‡]	(0.09)
Site 2	750	5.09*a*	(0.47)	4.45*a*[‡]	(0.10)
(Small spring entering control section at 725 m)		6.11*ab*	(0.45)	5.43*e*[‡]	(0.39)
Site 3	700	5.36*ab*	(0.62)	4.50*ab*[‡]	(0.10)
Site 4	600	5.42*ab*	(0.65)	4.52*ab*[‡]	(0.10)
Limed section					
Bar 1* (33.5 t)[†]	525	5.54*ab*	(0.72)	4.54*abc*[‡]	(0.10)
Bar 2 (16.7 t)	500	5.63*ab*	(0.76)	4.56*abcd*[‡]	(0.10)
Bar 3* (22.3 t)	460	5.76*ab*	(0.76)	4.60*abcd*[‡]	(0.14)
Bar 4* (23.5 t)	420	5.82*ab*	(0.77)	4.60*abcd*[‡]	(0.13)
Bar 5 (21.2 t)	375	5.92*ab*	(0.76)	4.63*abcd*[‡]*	(0.12)
Bar 6* (33.5 t)	300	6.03*ab*	(0.76)	4.69*bcd*[‡]	(0.17)
Bar 7 (22.3 t)	275	6.02*ab*	(0.75)	4.71*cd*[‡]	(0.16)
Bar 8 (26.7 t)	250	6.07*b*	(0.75)	4.76*d*[‡]	(0.18)
Mouth of brook	0	6.06*b*	(0.74)	4.76*d*[‡]	(0.19)
(Medway River)		5.66*ab*	(0.19)	5.52*e*	(0.41)
Water temperature (°C)		14.3	(3.9)	7.1[‡]	(5.1)
Water discharge ($m^3 \cdot s^{-1}$)		0.187	(0.071)	1.177	(1.728)

Note: Sites are identified on Fig. 1.

*Bars where limestone was replenished in 1991 with the same quantity as in 1987.

[†]Amount of limestone added to form each bar (1 t = 0.45 m^3).

[‡]Significant differences between pre- and post-episode means (*t*-test, $P < 0.001$).

[§]For a significant ANOVA ($P < 0.01$) within a column, means followed by the same letter are not significantly different (Tukey B multiple-comparison test, $P = 0.05$

electrofishing in August, before liming, were marked using a distinct fin clip for each of the four sections in which they were caught (i.e., four possible marks). Then in October, after liming, all fish caught were examined for fin clips, and their movements in the brook between August and October were determined based on the sections of origin and those of recapture.

In the past, Atlantic salmon all spawned within the area of Fifteen Mile Brook used as control and limed sections in this study (Lacroix 1985). Therefore, counts of Atlantic salmon redds in the brook were made annually from 1987 to 1994, except in 1991 when very high water flow prevented it. During November–December each year, weekly surveys for redds were made by wading along the brook from the mouth to beyond the control section, and the location of any new redds and changes made to existing redds were recorded. Because no salmon were found to spawn upstream of the control section, the distribution of all redds in the brook was known. In contrast, brook trout redds were found in all areas of the brook where fine bed material was available, but reliable counts could not be made. Brook trout redds were very small and usually difficult to identify in the brown water, especially after a period of high water flow.

Results

Effects of liming on water chemistry

The pH in Fifteen Mile Brook increased by about 0.05–0.10 pH units over each of the eight limestone bars resulting in a significant longitudinal pH gradient as water flowed from the first to the last limed area (Table 2). This increase in pH then persisted to the mouth of the brook, 250 m downstream of the last limestone bar. Before liming, there was no such gradient; for example, in August 1987, pH only varied from 5.95 at Site 1 to 6.0 at the mouth of the brook, and it was uniform throughout the section to be limed. The overall mitigative effect of the limed bars was > 0.5 pH units during pre-episode periods, but it was considerably less after acidic episodes. Interannual variability in pH at a site was high before episodes, and pH was usually significantly different only beyond the limestone bar furthest downstream. After episodes, interannual variability in pH was low, and there were significant differences in pH among many of the bars as pH increased downstream (Table 2). Acidic episodes always led to significantly lower pH levels at all sites along the brook where pH was measured. In the control section, a small groundwater-fed spring entering the brook part way through that section also resulted in a slight increase in pH downstream, especially during the low flow, pre-episode period. After episodes, the contribution by this spring to the discharge of the brook was small and the effects on pH were minimal. Water from the spring was clear, with low DOC (< 2 $mg \cdot L^{-1}$), and pH was always much higher in the spring than in Fifteen Mile Brook.

Increases in mean pH, ANC, [Ca], and [Mg] of water after flowing over the limestone were significant for the 8 years combined (Table 3). The increase in pH averaged 0.3 pH units, and mean [Ca + Mg] increased by 0.5 $mg \cdot L^{-1}$. Both [Ca] and [Mg] increased over the limed section because the limestone was dolomitic (i.e., magnesium based limestone), indicating

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Table 3. Water chemistry (mean concentration with SD given in parentheses) in control and limed sections of Fifteen Mile Brook after liming, from 15 September 1987 to 26 December 1994 (n = paired sample size).

	Control		Limed		n
pH	4.97	(0.56)	5.29*†	(0.70)	141
ANC‡ ($mg \cdot L^{-1}$ $CaCO_3$)	0.2	(1.4)	1.6*†	(3.1)	137
Na ($mg \cdot L^{-1}$)	3.53	(0.65)	3.54	(0.68)	137
K ($mg \cdot L^{-1}$)	0.15	(0.10)	0.15	(0.10)	137
Ca ($mg \cdot L^{-1}$)	0.96	(0.41)	1.31*†	(0.77)	137
Mg ($mg \cdot L^{-1}$)	0.57	(0.24)	0.72*†	(0.33)	137
Cl ($mg \cdot L^{-1}$)	5.0	(1.0)	5.0	(1.1)	137
SO_4 ($mg \cdot L^{-1}$)	2.8	(1.7)	2.8	(1.8)	137
F (range, $mg \cdot L^{-1}$)	0.01–0.02	0.01–0.02			15
DOC§ ($mg \cdot L^{-1}$)	12.9	(6.3)	12.7	(6.2)	136
SiO_2 ($mg \cdot L^{-1}$)	5.06	(3.99)	5.01	(3.94)	57
Al (total, $\mu g \cdot L^{-1}$)	159	(72)	156†	(69)	133
Al (exchangeable, $\mu g \cdot L^{-1}$)	12	(11)	10	(8)	84
Fe ($mg \cdot L^{-1}$)	0.55	(0.30)	0.54†	(0.29)	126
Mn ($\mu g \cdot L^{-1}$)	34	(17)	35	(17)	102
Cd ($\mu g \cdot L^{-1}$)	<1		<1		10
Cu (range, $\mu g \cdot L^{-1}$)	<1–1		<1–4		10
Pb ($\mu g \cdot L^{-1}$)	<1		<1		10
Zn ($\mu g \cdot L^{-1}$)	4	(1)	4	(1)	10

*Significant differences between sections (t-test, $P < 0.05$).
†Significant differences between sections (paired-sample t-test, $P < 0.01$).
‡ANC, acid neutralization capacity.
§DOC, dissolved organic carbon.

that the pH increase in the limed section was the result of liming and not because of input of spring or groundwater as in the control section. Seasonal fluctuations in pH were similar to those in [Ca + Mg], which increased most in the limed section at times of low water flow and high water temperature (Fig. 2). In both the control section and the limed section, episodes of low pH followed periods of high discharge, usually in autumn, and pH remained low throughout winter. Other episodes of increased discharge either in spring or during summer often, but not always, led to low pH. The difference in pH between control and limed sections (i.e., at site 4 and immediately downstream of bar 8) ranged widely (0.01–1.3 pH units) over the 8 yr (Fig. 2). These differences in pH between sections were always greatest during summer at high water temperature, and the highest pH levels generally occurred at the end of summer after extended periods of low water discharge. As a result, the difference almost always exceeded 0.5 pH units at some time during summer, but it was often < 0.2 pH units in autumn and winter (i.e., post-episode).

Concentrations of Na, K, Cl, SO_4, F, DOC, and SiO_2 were not significantly altered by the limestone bars (Table 3). Similarly, concentrations of potentially toxic metals such as Al (exchangeable), Cd, Cu, Mn, Pb, and Zn did not differ significantly upstream and downstream of the limed section. Significant statistical differences were found in Al (total), and Fe between control and limed sections, but only with the paired-sample t-test. Overall, the differences between means were extremely small (3 $\mu g \cdot L^{-1}$ for total Al, and 0.01 $mg \cdot L^{-1}$ for Fe). Differences in Al (total) were usually < 10 $\mu g \cdot L^{-1}$ and, with one exception, they were always < 35 $\mu g \cdot L^{-1}$. Differences in Fe were always < 0.1 $mg \cdot L^{-1}$. Neither Al (total) nor Fe were consistently higher or lower in one section than the other, and they were unlikely to lead to different biological effects between sections. In addition, concentrations of DOC were always > 5 $mg \cdot L^{-1}$, and at times they exceeded 20 $mg \cdot L^{-1}$. As a result, > 90% of the total Al was in organic, nonexchangeable forms considered to be nonlabile. Exchangeable Al concentrations were usually < 20 $\mu g \cdot L^{-1}$, and they were always < 50 $\mu g \cdot L^{-1}$.

On an annual basis, the differences in mean pH, ANC, [Ca], and [Mg] between control and limed sections were also significant in most of the 8 yr (Table 4). The differences between sections were greater in 1987–1989 after limestone was first applied and again in 1993 and 1994 after the limestone was replenished than in other years (i.e., 1990, 1991, 1992). Some interannual variations in Ca and Mg were significant within each section (Table 4). The mitigative effect of the limestone decreased from 1987 on, but in 1990 and 1991 it was reduced most because of severe washouts on four of the eight bars as a result of two episodes of extremely high discharge (13.3 and 24.6 $m^3 \cdot s^{-1}$) during those years (Fig. 2). Replenishment of limestone on those four bars in November 1991 did not immediately lead to increases in the parameter differences between limed and control sections for the remainder of 1991 nor in 1992 because an episode of extremely high discharge occurred within 1 week of adding the limestone in November 1991 (Fig. 2). As a result, a portion of the limestone on these replenished bars was displaced to the banks and remained dry and ineffective after the high water receded. This limestone was raked back into the brook in the summer of 1993, after which it led to larger differences in pH, ANC, and [Ca + Mg] in 1993 and 1994 than in 1990–1992.

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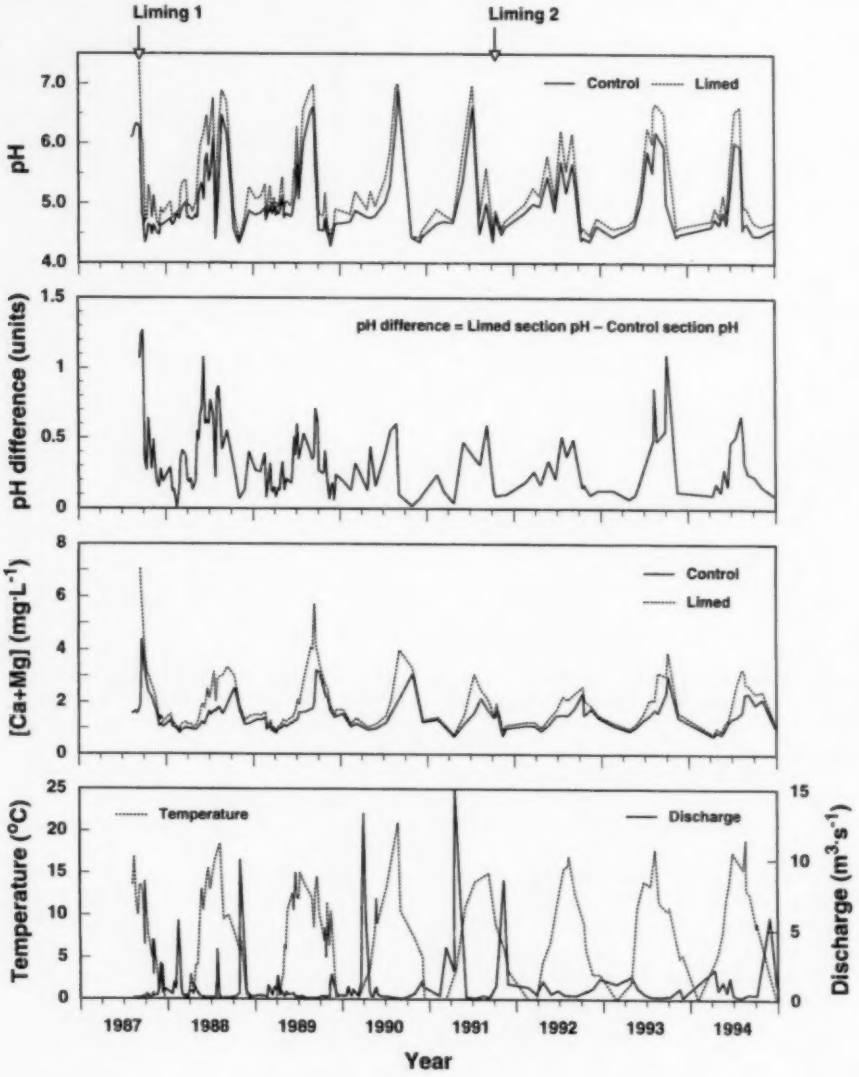
Fig. 2. Water pH in control and limed sections, the difference in pH between sections for paired samples, water Ca + Mg concentrations in control and limed sections, and water temperature and discharge in Fifteen Mile Brook from 1987 to 1994. Dates of limestone applications are also indicated (liming 1 = 200 t, liming 2 = 100 t).



Distribution and density of redds and fish

Adult Atlantic salmon generally entered Fifteen Mile Brook from the Medway River over several weeks during spawning in late November. Spawners did not avoid entering the brook at a time when pH levels were lowest (Fig. 2) and considerably lower than in the Medway River (Table 2). There were few large, deep pools where adult salmon could hold in the brook (Table 1), and they did not enter or remain in the brook at other times.

The number of redds made by spawning Atlantic salmon was always significantly greater in the limed section than in the control section (Table 5). Over the 7 yr when counts were made, 78% of the redds were dug in the limed section. Redds were usually, but not exclusively, placed on the limestone bars rather than on other gravel bars within the limed section. In the control section, redds were placed in gravel bars at the downstream end of pools or along the edge of runs. The limestone used was 4-cm grade, and it was finer than the average bed material normally available in both control and limed sections (Table 1). There was an absence of large beds of imported material of similar size in the control section.

A large proportion of the populations of juvenile Atlantic salmon and brook trout were marked in both the control section and the limed section in August 1987, before liming (Table 6). At that time, pH was high in both sections (Fig. 2), and fish of both species were relatively abundant in both sections

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Table 4. Interannual variations in mean water chemistry for parameters that were significantly different (Table 3) between control and limed sections of Fifteen Mile Brook.

	1987	1988	1989	1990	1991	1992	1993	1994
pH								
Control section	4.70	5.03	5.01	4.97	4.91	4.96	5.19	4.86
Limed section	5.21	5.42	5.29	5.19	5.14	5.21	5.50	5.15
Difference	0.51*	0.39*	0.28*	0.22*	0.23*	0.25*	0.31*	0.29*
ANC† ($mg \cdot L^{-1}$ $CaCO_3$)								
Control section	−0.31	0.35	0.59	0.30	−0.20	0.08	0.44	−0.08
Limed section	2.08	1.65	1.94	1.42	0.76	0.81	1.84	1.24
Difference	2.39*	1.30*	1.35*	1.12	0.96*	0.73*	1.40*	1.32*
Ca ($mg \cdot L^{-1}$)								
Control section	1.36*a*	0.82*b*	0.96*ab*	0.93*ab*	0.88*b*	0.95*ab*	1.01*ab*	0.96*ab*
Limed section	2.05*a*	1.16*b*	1.31*ab*	1.18*b*	1.10*b*	1.13*b*	1.34*ab*	1.27*ab*
Difference	0.69*	0.34*	0.35*	0.25	0.22*	0.18*	0.33*	0.31*
Mg ($mg \cdot L^{-1}$)								
Control section	0.84*a*	0.49*b*	0.56*b*	0.57*b*	0.47*b*	0.57*b*	0.59*b*	0.56*b*
Limed section	1.04*a*	0.64*b*	0.73*ab*	0.68*b*	0.58*b*	0.67*b*	0.73*b*	0.70*b*
Difference	0.20*	0.15*	0.17*	0.11*	0.11*	0.10*	0.14*	0.14*
n	14	33–34	34–36	10–11	10	12	10	14

Note: For a significant ANOVA ($P < 0.05$) within a row, means followed by the same letter are not significantly different (Tukey B multiple-comparison test, ($P = 0.05$).

*Significant differences between sections in separate years (paired-sample *t*-test, $P < 0.05$).

† ANC, acid neutralization capacity.

Table 5. Number of Atlantic salmon redds in control and limed sections of Fifteen Mile Brook after spawning in autumn from 1987 to 1994.

	Number of redds	
	Control section	Limed section
1987	3	22*
1988	3	13*
1989	11	20*
1990	1	9*
1991	—	—
1992	5	13*
1993	4	15*
1994	3	15*
Mean (SD)	4.3 (3.2)	15.3† (4.4)

Note: Redds were not counted in 1991 because of high water flow.

*Distributions within a year significantly different from equality (chi-square, $P < 0.05$).

†Significant difference between sections for overall means (*t*- test, $P < 0.05$).

(Figs. 3 and 4). After liming, the number of fish caught in October 1987, after pH had decreased, was considerably reduced, more so in the control section than in the limed section. However, a high proportion (about 60%) of the juvenile salmon had marks indicating residence in the brook. Brook trout apparently moved more than juvenile salmon because the proportion of brook trout considered to be resident after the acid episode was about 30%. A greater proportion of fish of both species were resident in the control section than in the limed section after the acid episode. Very few of the fish marked before liming moved between sections after liming and after the acid episode (Table 6). The majority of fish of both species considered resident of the brook remained within the section in which they were originally marked. Of the fish that moved between sections, twice as many age–0 salmon moved from the control section to the limed section than vice versa after the pH decreased. Movements of brook trout between sections were about equal in both directions.

Over the 8 yr of monitoring, there were large interannual variations in the density of juvenile Atlantic salmon in Fifteen Mile Brook, and there was no trend over time (Fig. 3). Before liming, juvenile salmon were absent from the brook after the annual acidic episode (i.e., in October 1986), but they were present in similar numbers throughout the area later to be subdivided into a control and a treatment during the summer period of high pH (i.e., in August 1987). After liming, age–0 salmon were always more abundant in the limed section than in the control. Age–0 salmon accounted for > 90% of the total salmon density, and few age–1 and older salmon (< 0.02 $fish \cdot m^{-2}$) were present in the brook at any time. The density of age–1 and older salmon usually did not differ much between sections.

The same interannual variations in juvenile salmon density occurred in both control and limed sections. Densities were, therefore, examined in relation to the minimum pH levels attained in control and limed sections of the brook during the period before the estimate of fish density (Fig. 3). For example, the period before the August sampling date was from the start of fry emergence (i.e., at the end of May). These minimum pH levels were always lower in the control section than in the limed section. As a result, the density of age–0 salmon was always higher in the limed section than in the control section. Without exception, juvenile salmon were present after periods of high minimum pH in both sections. However, they were rare in the limed section and often absent in the control section after periods when minimum pH was lowest. This was

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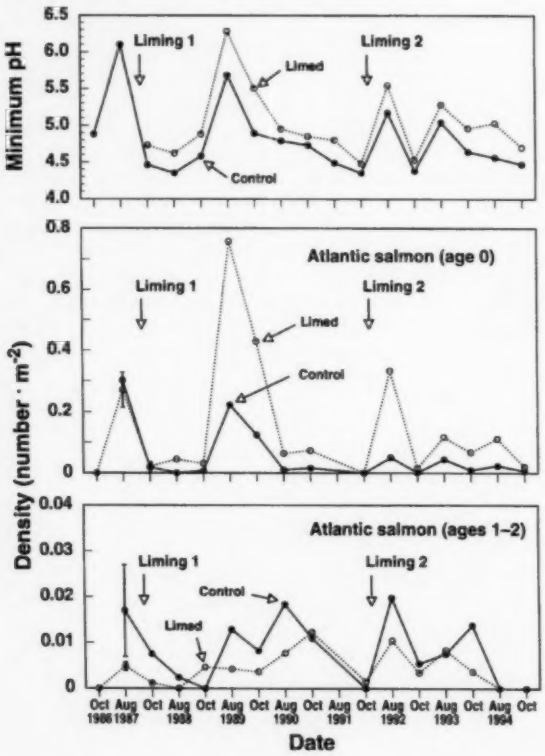
Table 6. Distribution and movements of juvenile Atlantic salmon and brook trout between sections of Fifteen Mile Brook before and after liming during 1987.

	No. of fish marked in August			No. of fish caught in October			No. of fish moving between sections		
	Control	Pre-limed[a]	Total	Control (% marked)[b]	Limed (% marked)[b]	Total (% marked)[b]	Limed–control	Control–limed	Total
Atlantic salmon									
Age 0	235	309	544	20 (75)	35 (49)	55 (58)	3	6	9
Ages 1–2	12	6	18	4 (75)	1 (0)	5 (60)	0	0	0
Brook trout									
Age 0	249	217	466	92 (40)	158 (27)	250 (32)	3	4	7
Ages 1–4	79	100	179	26 (38)	79 (27)	105 (30)	1	1	2

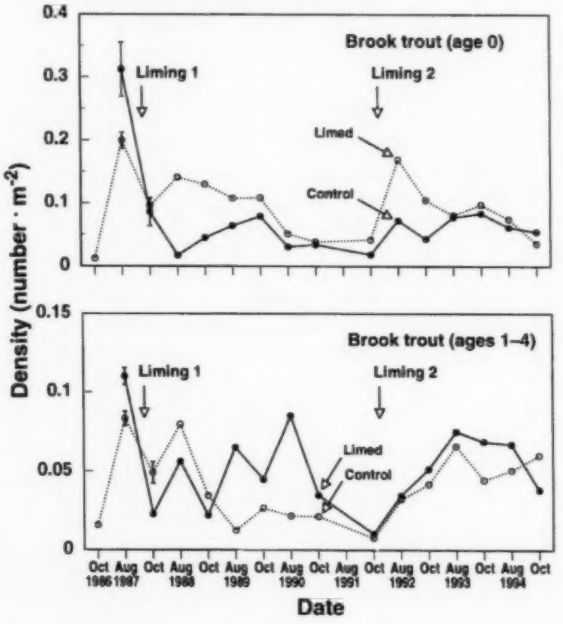
[a] Section where fish were caught before liming later in September 1987.
[b] Percent of fish caught in October in each section previously marked in August.

Fig. 3. Minimum pH in the intervals before density estimates, and densities of age–0 and age–1 plus age–2 Atlantic salmon in control and limed sections of Fifteen Mile Brook estimated in August and October from 1986 to 1994. Vertical bars around means in 1987 indicate range of densities within a section. Dates of limestone applications are also indicated.



usually in October, when density was estimated after the annual acidic episode. On 10 occasions, minimum pH was < 4.8 in the control section during the period before density was estimated, and in each case juvenile salmon were either absent

Fig. 4. Densities of age–0 and age–1 to age–4 brook trout in control and limed sections of Fifteen Mile Brook estimated in August and October from 1986 to 1994. Vertical bars around means in 1987 indicate range of densities within a section. Dates of limestone applications are also indicated.



or density was ≤ 0.02 fish·m^{-2}. In contrast, minimum pH was < 4.8 on only five occasions in the limed section; densities of juvenile salmon were also lowest at those times, but they were only absent on one occasion. At all other times, minimum pH in the limed section was high enough to allow some survival of age–0 and older salmon (Fig. 3).

The density of juvenile salmon in the limed section was highest in 1989, 2 yr after first liming, but it decreased again in the following 2 yr (1990 and 1991) when pH was low, and the pH difference between the control and limed sections had decreased. No age–0 salmon were found in either section, and

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only one age–1 parr was found in the limed sections after episodes of extremely high discharge and low pH in 1991 (Figs. 2 and 3). The density of juvenile salmon increased again in 1992 when pH levels were high and when the pH difference between sections increased after the second application of lime. Densities were low again in 1993 and 1994, but the difference in pH between sections remained high enough for the limed section to support significantly more age–0 salmon than the control section. The average density of juvenile salmon over 8 yr after liming was 0.153 fish·m^{-2} in the limed section compared with 0.046 fish·m^{-2} in the control section. Only in August and October 1989 and August 1992 and 1993 did densities in each section approach or exceed these averages. Those were the periods with the highest pH levels in both sections. High pH levels in August 1987, before liming, were also associated with densities above average.

In contrast to juvenile salmon, some brook trout were always present in the brook regardless of pH. However, interannual variations in the density of brook trout were similar to, but not as marked as, those for juvenile salmon (Fig. 4). The similarity over time was especially evident for age–0 fish. Only in 1989 did the density of age–0 brook trout not increase to the extent that the density of age–0 salmon did. Both the highest and lowest densities of brook trout (all ages) occurred in the year before liming, and densities in the control section were higher than in the section to be limed. The decrease in density of brook trout of all ages immediately after liming was associated with the lowest minimum pH levels in October 1987. Thereafter, the density of age–0 brook trout was always greater in the limed section than in the control section, except in October 1994 (Fig. 4); the difference in density between sections was greatest in the year after first liming (1988) and in the year after the second limestone addition (1992). By the end of the study (1993–1994), densities of brook trout of all ages were very similar in both sections. The lowest densities of age–0 brook trout (< 0.05 fish·m^{-2}) occurred in 1990–1991, both years when minimum pH levels were low with the smallest differences in pH between sections. Those were also the years with episodes of extremely high discharge in the brook (Fig. 2). The density of age–1 and older brook trout also reached its lowest level (< 0.01 fish·m^{-2}) after the worst episodes in 1991. The density of age–1 and older brook trout, like that of age–1 and older salmon, did not differ much between sections, but it was usually slightly higher in the control section than in the limed section after 1988.

The average density of brook trout of all ages over 8 yr after liming was 0.130 fish·m^{-2} in the limed section compared with 0.103 fish·m^{-2} in the control section. Densities in each section were usually near those averages, except in 1988 in the control section and in 1990–1991 in both sections. In 1988, pH levels in the control section were < 4.6 and those in the limed section were above that level, whereas in 1991, pH levels were < 4.5 in both sections. The average density of brook trout (all ages) after liming was more than twofold that of juvenile salmon (all ages) in the control section. Only in 1989, when pH levels were high in the control section, were age–0 salmon more abundant than age–0 brook trout. In the limed section, differences in average density (all ages) between species were not as great and juvenile salmon were more abundant (1.2×) than brook trout. The very high densities of age–0 salmon in the summers of 1989 and 1992, compared with those of brook trout, accounted for most of this difference. At those times, pH levels were highest in the limed section. At most other times, densities of age–0 brook trout were either similar to or greater than those of age–0 salmon, and densities of age–1 and older brook trout were always greater than those of age–1 and older salmon in the limed section. Few age–1 and older salmon remained in the brook in contrast to the number of age–1 and older brook trout present. This difference was also obvious before liming. For example, the ratio of age–0 to older fish was 30.2:1 for juvenile salmon compared with 2.6:1 for brook trout throughout the brook in August 1987 (Table 6).

Discussion

Applying limestone gravel to the bed of Fifteen Mile Brook led to changes in water chemistry in the limed section and downstream and, therefore, to differences between the limed section and the control section. The method and the amount and size of limestone used (i.e., initial application plus partial replenishment after 4 yr to maintain a constant amount) were effective in maintaining a small increase in pH at all times, without changing the natural seasonal variations linked to water discharge and the input of organic acids (Lacroix 1992). The result was a change similar to what would be anticipated in the brook from a decrease of excess, non-marine SO_4 input as a result of reductions in atmospheric deposition. Conditions were, therefore, well suited to study the potential for recovery of fish communities in the brook if SO_4 deposition was to decrease.

The limestone was most effective at low water flow and high water temperature (i.e., pre-episode), but a small pH difference was always maintained even at the very low pH that occurred during periods of high flow in autumn and during winter (i.e., post-episode). This difference in effectiveness was apparently related to water flow because of its effect on water volume being limed and contact time with the limestone, and also related to water temperature because of its effect on reactivity and rate of dissolution of the limestone. Extensive monitoring of water chemistry before liming (i.e., control in time) was not necessary to ascertain the impact of liming because of the unique chemical signature of the limestone used. Increases in both Ca (26%) and Mg (36%) led to the changes in ANC and pH in the limed section indicating that the dolomitic limestone (i.e., high in Mg in addition to Ca), and not dilution by groundwater or spring water low in organic acids, was responsible for the change and gradient of increasing pH along the limed section. A small increase in pH did occur in the control section immediately downstream of where a small, clear-water spring entered the brook. Mixing was rapid, and no other changes occurred along the 100-m reach of the control section furthest downstream. The mitigative effects of spreading limestone over a several small bars were similar to those observed by Keller and Gunn (1982) after placing a single, large barrier of crushed limestone in a small seasonally acidic stream, except that they only found a large increase in Ca, and not Mg, because they were using Ca-based limestone. Keller and Gunn (1982) also found that total concentrations of Al, Fe, and Mn decreased below the barrier indicating that the metals were precipitated as a result of the increase in pH to near neutral. Total Al and Fe in Fifteen Mile Brook were only marginally lower in the limed section. These metals were mostly in non-

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exchangeable forms (e.g., 90% of total Al) and bound to organic anions that were present in high concentrations, as indicated by DOC. The speciation of metals such as Al did not change with the small increase in pH from liming, and Al would not have precipitated with the pH difference observed between sections (Driscoll 1989). Seasonal changes in total Al and Fe always closely paralleled those in DOC (Lacroix 1992).

The increases in pH, ANC, and [Ca + Mg] in the limed section of the brook was found to decrease gradually over the first 3 yr (Lacroix 1992). Additional monitoring in this study showed that some mitigative effect persisted over the 8 yr indicating the potential for this technique over the long term. However, the limestone had to be partially replenished once after 4 yr when severe floods washed out some of the bars. The second application was limited to the areas where it had washed out, and the quantity of limestone used was the same as that initially applied to those areas. The largest impact of the limestone occurred in 1987–1988 after the first application and in 1993 after the second application was spread back out. Effectiveness then decreased over time as the limestone became coated with organic matter and as some of it was pushed along the edges of the brook by high flows (e.g., in 1991 immediately after the second application), indicating a need for some maintenance at intervals of 2 or 3 yr (i.e., raking to stir and remove coating from limestone and to spread limestone back into the main flow).

Liming resulted in changes in the density of fish in the limed section and to differences in the distribution and density of redds and fish between the control section and the limed section. In a preliminary evaluation of the method, Lacroix (1992) suggested that trends indicative of recovery for juvenile salmon, and to a lesser extent brook trout, were developing. This was premature, and the additional monitoring over 8 yr indicated that there were no such trends over time in the number of salmon redds, nor in the densities of any age-class of juvenile salmon and brook trout. However, liming did have some positive effects on the fish community, but the changes in fish densities in the limed section were entirely dependent upon year-to-year variations in the severity of acidic episodes. Because of the lack of trends, the absence of a long period of monitoring of fishes before liming (i.e., control in time) did not create a void that the comparison of a limed section with a control section (i.e., control in space) could not fill for interpreting the impact of liming.

Atlantic salmon consistently placed most of their redds (78%) in the limed section, and these were most often on the limestone bars. In a survey of redd locations throughout Fifteen Mile Brook conducted in 1980, Lacroix (1985) observed that, before liming, redds were distributed throughout the area from the mouth of the river to what was later selected as the upstream boundary of the control section. Lacroix (1985) also found, during a study of egg survival in artificially built redds, that wild salmon selectively spawned in the areas where the artificial redds had previously been dug, probably because of the reduced compaction and increased permeability of the streambed. The aggregation of redds in the limed section may have occurred because of the ease with which salmon could dig redds in the bars of loose, permeable limestone gravel rather than because of the difference in pH between sections or because of any attraction to less acidic conditions. No gravel of similar size, but with different geology, was spread in the control section to provide a similar choice. Adult Atlantic salmon did not avoid low pH, but entered Fifteen Mile Brook every autumn to spawn despite the more acidic conditions at the mouth of the brook than in the Medway River at those times.

The deposition of eggs by Atlantic salmon in limestone beds could have led to an increase in the survival of eggs and alevins incubated in the limestone over that previously measured by Lacroix (1985) under acidic condition in Fifteen Mile Brook, because of the relationship between egg survival and the pH of interstitial water in gravel bars. This could have been a reason for the higher initial densities of age–0 salmon in the limed section than in the control section in the summer before acidic episodes reduced their numbers. Incubation of salmonid eggs in limestone gravel in acidic water was found to reduce the mortality of embryos and alevins (Gunn and Keller 1980). Lacroix (1992) observed that the pH of interstitial water in Fifteen Mile Brook, normally pH 5.4, was increased to neutral (pH 7.1) in the limestone bars where the majority of Atlantic salmon dug redds and spawned.

Acidic episodes always resulted in a large loss of fish in control and limed sections of the brook, either through increased emigration or mortality. No juvenile salmon and few brook trout remained after the episodes of lowest pH. The high proportion of resident juvenile salmon remaining after an acidic episode (60%) would tend to indicate that mortality, rather than emigration, was high. In contrast, the low proportion of resident brook trout (30%) after an episode would indicate that emigration may have been more extensive than mortality. Movements of fish between sections were rare. The higher degree of residence in both control and limed sections for Atlantic salmon compared with brook trout is supported by the observations that juvenile Atlantic salmon did not avoid low pH in a laboratory study whereas brook trout did show low pH avoidance (Peterson et al. 1989). Salmon that failed to avoid episodes of low pH below lethal levels, by emigrating downstream to the main river, would most likely have died.

Before liming, juvenile Atlantic salmon were absent in Fifteen Mile Brook after acidic episodes but a few brook trout remained in the brook as observed in October 1986 (this study), and in November 1986 and January 1987 (Lacroix et al. 1990). However, the physiological responses of brook trout at those times indicated that they were stressed by the low pH (Lacroix et al. 1990). After liming, the same situation persisted in the control section over the 8 yr; on 10 occasions, episodes with pH < 4.8 occurred before density was measured, on 2 of these occasions age–0 salmon was absent and on the other 8 occasions their density was extremely low (< 0.02 fish·m^{-2}). The effect of liming was to reduce the number of episodes with pH < 4.8 to five occasions (i.e., 50% less than in the control section); on these occasions the density of age–0 salmon in the limed section was also low but not as low as in the control section. At all other times, liming had a markedly positive impact on the density of age–0 salmon in comparison with densities in the control section. Liming, therefore, allowed age–0 salmon to survive in years with low pH in summer and many of the severe acidic episodes that occurred in autumn. In addition to the difference in pH between sections, the increase in [Ca] in the limed section at the low concentrations found in the brook could also have enhanced fish survival because of its role in reducing physiological stress caused by

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ion loss at the gills (McDonald et al. 1980; Brown 1983; Hunn 1985). The densities of age–1 and older salmon were always so low that differences between sections were not apparent, but they were usually also absent in years with low minimum pH.

The responses of the brook trout population to liming and to temporal variations in pH were similar to, but not as pronounced as, those of juvenile salmon. Unlike salmon, some brook trout of all ages were always present in the brook even after periods of pH < 4.5. They were more abundant in both sections in years with the highest minimum pH, and age–0 trout were more abundant in the limed section than in the control, but the differences were small except in the years immediately after the first and second liming. The extremely high flows and low pH that resulted in a near total absence of juvenile salmon in 1991 were also devastating to the trout population, especially the older age-classes, in both sections of the brook. Brook trout of age–1 and older were always more abundant than salmon of the same age. They were found equally in both sections and occupied the deeper pool areas that were probably the determinant factor in their distribution (Lacroix et al. 1995). Differences in the distribution of age–0 salmon and brook trout pointed towards a greater tolerance of brook trout to low pH. In the limed section, age–0 salmon were more abundant than brook trout of the same age in the years with minimum pH > 4.8. In the control section, age–0 brook trout were usually more abundant than age–0 salmon, except in 1989, the year with the highest minimum pH before densities were estimated in that section. Brook trout tolerated lower pH levels than juvenile salmon. A similar difference in tolerance was previously indicated by observations at the community level (Lacroix 1987) and by the physiological responses of these two species to low pH (Lacroix 1989*c*; Lacroix et al. 1990). Keller and Gunn (1982) found no differences in survival of brook trout upstream and downstream of a limestone barrier, but the relatively high pH (> 5.3) before liming would not have had a major impact on the brook trout. In contrast, Gagen et al. (1989) found that mitigation of low pH with alkaline groundwater in an acidified stream (i.e., from pH 4.9 to 6.0) resulted in colonization by brook trout and permanent changes in density. However, comparing the relative sensitivities of brook trout among studies may be difficult because of the considerable variability in acid resistance between strains of brook trout (Robinson et al. 1976; Swarts et al. 1978).

Interannual variations in the densities of age–0 salmon and brook trout were almost identical in both sections and they followed the seasonal and annual variations in minimum pH, regardless of the differences in density or in pH between sections. There were also some similarities in year-to-year variations in density for older fish of both species. With only a few salmon redds in the control section in all years but one, the presence of juvenile salmon in that section had to be partly from immigration, most likely of fish that survived in the limed section. At times when few or no juvenile salmon survived in a section, minimum pH had been below levels leading to mortality of juvenile salmon in other rivers of Nova Scotia where episodes with pH < 4.5 for several days or pH 4.5–4.7 for extended periods were lethal (Lacroix and Townsend 1987; Lacroix 1989*b*). As a result of the high DOC and high covariance between DOC and total Al (Lacroix 1992), concentrations of exchangeable, i.e., potentially labile, Al were usually < 20 $\mu g \cdot L^{-1}$ in these waters dominated by organic acids. Aluminum was, therefore, unlikely to be responsible for the lethal effects observed as also indicated by the physiological responses of fish in Fifteen Mile Brook (Lacroix et al. 1990) and in other rivers with similar chemistry (Lacroix 1989*b*).

Evaluation of the stability and performance of separate bars indicated some criteria for site selection. The bars selected for adding crushed limestone should be shallow to provide a large surface area for water contact and percolation through the gravel. Bars located in wide, straight, and shallow channel sections were more stable and effective than bars in narrow, winding, deep sections that were less stable and lost limestone downstream to pools where it probably became relatively ineffective as a result of decreased percolation and contact. Limestone gravel was best applied during periods of low flow in late summer to facilitate access and to minimize effects on habitat. The environmental intervention associated with the application of limestone on the streambed did not decrease the variability of habitat available compared with that in the control section, nor did it alter the habitat (i.e., water depth, focal water velocity, and bed material) used by juvenile salmon and brook trout (Lacroix et al. 1995). Distribution of the limestone over a number of bars did not create a barrier to the movement of fish. This would seem preferable to the method used by Pearson and McDonnell (1975) or by Keller and Gunn (1982) where a single large limestone barrier was built.

The level of intervention, effort, or maintenance to use this method was very small and inexpensive when compared with other methods used to lime running waters, but the increase in pH was relatively small. In contrast, the application of powdered limestone to neutralize headwater lakes has the advantage of increasing pH to a greater extent in outlet streams throughout the year and in maintaining a larger increase throughout periods of high water flow, but it needs to be repeated annually at a high cost compared with streambed liming (Watt et al. 1984; Lacroix 1995). The streams are also vulnerable to interruptions in annual treatment because, in its absence, pH generally returns to preliming levels very rapidly. Episodic events could then lead to very large, rapid decreases in pH and to severe impacts on fish acclimated to circumneutral conditions.

In conclusion, the application of crushed limestone to form bars on the bed of a small acidic stream was successful as a long-term mitigation strategy to moderately increase pH. Although the pH of running water was increased only by a small amount, especially at times of high water flow, it was sufficient for some juvenile salmon and brook trout to survive severe, otherwise lethal, acidification episodes in the brook. The limestone bars improved the spawning habitat by providing superior physical substrate for salmon to dig redds, and also by increasing the pH of interstitial water over eggs and alevins (Lacroix 1992). Together, these changes probably resulted in the large increases in the density of juvenile salmon and, to a lesser extent, brook trout observed in some years in the limed section of the brook. The benefits of this mitigative strategy were attained without serious adverse effects on the environment nor on the habitat features used by juvenile salmon and brook trout (Lacroix et al. 1995). This study indicated that small-scale applications of limestone to the streambed in nursery areas could be used to mitigate low pH and

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some of its adverse effects on salmonids over a long time period with minimal maintenance requirements. However, the degree of success was limited by the small margin of chemical recovery during acidic episodes. The mitigation strategy used has shown that survival of juvenile Atlantic salmon and brook trout can be improved at much lower levels of recovery from acidification than previously considered.

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Landscape-scale influences on stream habitats and biota

Carl Richards, Lucinda B. Johnson, and George E. Host

Abstract: The relative influence of geologic versus anthropogenic attributes of catchments on stream ecosystems was examined in 45 catchments of a river basin in central Michigan. Each catchment was characterized by land use, surficial geology, elevation, and hydrography, and summaries of these data were related to physical habitat characteristics that had the greatest influence on macroinvertebrate assemblages. Partial redundancy analysis revealed that geologic and land-use variables had similar magnitudes of influence on stream habitats. Of the geologic variables, catchment area, proportion of lacustrine clays, and glacial outwash materials had the strongest influence on physical habitat, particularly on channel dimensions. Row-crop agriculture and the presence of wetlands were the most important land-use variables, particularly influencing amounts of woody debris. Stream buffers (100 m) were more important than whole catchment data for predicting sediment-related habitat variables; however, channel morphology was more strongly related to whole catchments. Results suggest that catchment-wide geology and land-use characteristics may be more important than stream buffers for maintaining or restoring stream ecosystems. These techniques can be used to develop biologic signatures of catchment condition that discriminate causal factors influencing the biodiversity and health of stream ecosystems.

Résumé : Nous avons examiné les influences respectives sur les écosystèmes des cours d'eau des attributs géologiques des bassins-versants en regard de leurs attributs anthropiques dans 45 aires d'alimentation d'un bassin fluvial du centre du Michigan (États-Unis). Nous avons caractérisé chaque aire d'alimentation par l'utilisation du sol, la géologie de subsurface, l'élévation et l'hydrographie et nous avons rattaché les sommaires des données ainsi obtenues aux caractéristiques de l'habitat physique qui exerçaient la plus forte influence sur les communautés de macro-invertébrés. L'analyse par redondance partielle a révélé que les variables géologiques et les variables d'utilisation du sol exerçaient sur les habitats une influence du même ordre de grandeur. Pour ce qui est des variables géologiques, ce sont l'aire du bassin-versant ainsi que la proportion d'argiles lacustres et de matériaux stratifiés fluvio-glaciaires qui ont agi le plus sur l'habitat physique, particulièrement sur les dimensions du chenal. Les cultures en lignes et la présence de terres humides consituaient les plus importantes variables en matière d'utilisation du sol, variables qui ont agi tout particulièrement sur la quantité de débris ligneux. Les zones tampons (100 m) ont joué un plus grand rôle que les données sur les bassins-versants tout entiers dans la prévision des variables d'habitat relatives aux sédiments; par contre, la morphologie du chenal se rattachait plus fortement aux bassins-versants tout entiers. Les résultats permettent de penser que la géologie du bassin-versant et les caractéristiques d'utilisation du sol font peut-être plus que les zones tampons pour maintenir ou rétablir les écosystèmes des cours d'eau. On peut recourir à ces techniques pour élaborer, au sujet de l'état des bassins-versants, des signatures biologiques qui distinguent les facteurs causaux de la biodiversité et de la santé des écosystèmes des cours d'eau.
[Traduit par la Rédaction]

Introduction

The biotic composition of streams is strongly influenced by physical habitat. Stream habitats provide the template upon which the ecological organization and dynamics of lotic ecosystems are observed (Minshall 1988; Resh et al. 1988; Poff and Ward 1989; Townsend and Hildrew 1994) and alteration of these habitats can have dramatic and persistent impacts on biotic assemblages (Niemi et al. 1990). Habitats are influenced by factors operating at a number of spatial and temporal scales. At regional scales, geomorphology and climate affect stream hydrology, sedimentation, nutrient inputs, and channel morphology (Hughes et al. 1994). At more local scales, land use, through alteration of stream habitats, can have significant influences on macroinvertebrate assemblages (e.g., Richards and Host 1994). Consequently, the identity and prediction of land-use impacts on stream habitats are essential components of resource management. Conservation and restoration strategies depend on this knowledge.

Separating the impacts of land use from other catchment-scale features is difficult. The physical characteristics of streams are influenced by a variety of landscape features, many of which are intercorrelated. The terrestrial basin, defined by the areal extent and distribution of geologic features (e.g., surficial geology, topography), can influence hydrology and sediment inputs to stream channels. Vegetative cover, which is determined in part by geomorphic factors (Host and Pregitzer 1992), moderates the amount of water, organic materials, and inorganic materials streams receive. Variation in land use, land cover, and basin morphology results in spatial heterogeneity at the terrestrial–aquatic ecotone (Forman and

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Godron 1986; Schlosser 1991). Lateral linkages, associated with the width, extent, and composition of riparian zones, mediate the delivery of sediments, nutrients, and allochthonous materials into stream channels (Keller and Swanson 1979; Bisson et al. 1987). Longitudinal linkages result from energy fluxes associated with the downhill movement of water, altered channel dimensions, and the rates of sediment transport (Richards 1982; Leopold et al. 1964).

A well-developed body of theoretical literature exists on the hierarchical organization of stream habitats (e.g., Frissell et al. 1986; Minshall 1988; Fitzgibbon and Imhof 1994). At large scales, geologic and climatic differences among basins determine the dominant physicochemical characteristics. Regional landscapes are divided into major drainage basins that define specific river systems and are further subdivided to include smaller catchments that define lower order streams. Subsequent subdivisions of stream systems are defined by larger morphological features of stream reaches, e.g., percent deep pools and percent riffles. These subdivisions are further distinguished by smaller habitat features, e.g., pool depth and substrate type. Each finer scale is expected to incorporate factors that more proximally influence the biotic assemblage.

While hierarchy theory is well-established in the ecological literature (Allen and Starr 1982), there are few empirical studies that assess the strength of relationships between land use and other environmental variables operating at different temporal and spatial scales. This study identifies catchment-scale geologic and anthropogenic factors that, through their influence on the physical habitat of streams, affect the structure and composition of the macroinvertebrate assemblages. Our goal was to use empirical relationships to identify patterns that exist at different scales of observation.

Methods

Study area

This study was conducted in the Saginaw Basin of Lake Huron in east-central Michigan. Drainages within the Saginaw Basin range from heavily impacted agricultural to relatively undisturbed forested areas. Geologically, the area consists of low-relief lacustrine and outwash plains, surrounded on the east and west by topographically complex end moraines. Soils of the lake plain are dominated by medium- and fine-textured loams and clays, with sand in the outwash plains and channels. The clay regions are extensively drained by artificial drainage and tile systems. Coarse-textured glacial features such as moraines and outwash plains are common in the basin's periphery. These peripheral regions contain a high percentage of forested land, whereas the low relief areas are dominated by agriculture. Catchments adjacent to Lake Huron (Kawkawkin and Coastal Basin streams) are characterized by low topographic relief and elevations averaging about 205 m. The Flint and Chippewa–Pine basins average about 278 m in elevation and exhibit the greatest variation in topography within the study area (Michigan Department of Natural Resources 1988).

The Saginaw Basin, which covers 16 317 km^2, encompasses four major basins: the Tittabawassee (6734 km^2), Shiawassee (3626 km^2), Flint (3108 km^2), and Cass (2331 km^2) rivers. The Tittabawassee River has two principal tributaries: the Chippewa River and the Pine River. Our study focuses on streams within five major basins of the Saginaw drainage: the Cass, Flint, Shiawassee, and Chippewa–Pine, and the Kawkawlin. In addition, we sampled several small catchments that flow directly into Saginaw Bay of Lake Huron; these are collectively referred to as the Coastal Basin (Fig. 1).

Study design

For this study, we selected 46 sites located on second- to third-order streams and delineated a unique catchment for each site. Sites were selected to reflect the range of land-use and physiographic conditions in the Saginaw Basin based on ground surveys and available knowledge. Biological and physical data were obtained for a 200-m stream segment at each site. Land-use patterns, hydrography, surficial geology, and elevation data bases were used to quantify several aspects of landscape structure. Specific sampling methods for each set of variables are described below.

Macroinvertebrate sampling methods

We used Hester–Dendy artificial substrate samplers (Ohio EPA 1987) to characterize macroinvertebrate assemblages. These samplers mimic hard substrates that support the majority of biotic production in soft bottomed streams (Benke et al. 1984). Colonization samplers have been used extensively to examine macroinvertebrate assemblages in streams (see Mackay 1992) and work well for depicting differences among sites (Yoder and Rankin 1995*a*). Modde and Drewes (1990) found that dominant assemblage characteristics from artificial plate samplers were similar to those found on natural hard substrates. Samplers were placed in early summer and again during base flow conditions early fall in 1991 or 1992. Three samplers were affixed to a concrete block and one or two blocks were deployed at each sampling site. Each sampler colonized for 6–8 wk. In the laboratory, all macroinvertebrates were counted and identified to genus whenever possible. A series of descriptive assemblage variables were calculated from the original species abundance data to describe assemblage composition (Table 1). Variables were chosen based on their relative utility for characterizing macroinvertebrate assemblages as suggested by Barbour et al. (1992) and Karr and Kerans (1992). We combined macroinvertebrate data from similar seasons of 1991 and 1992; preliminary analysis indicated no significant differences between sampling years at stations for which we had 2 yr of data (C. Richards, L. Johnson, and G. Host, unpublished data). Other work has shown that temporal variation in macroinvertebrate assemblages among catchments is greater among catchments than within catchments (Townsend et al. 1987; Weatherly and Ormerod 1990; Richards and Minshall 1992).

Physical habitat characterization

We assessed physical habitat during base flow conditions along a 200-m reach at each site. Using variables that are typically used to characterize stream habitats (Osborne et al. 1991; Richards and Host 1994), we sampled a suite of habitat measurements at each site, including cross sectional and longitudinal channel dimensions, substrate characteristics, bank conditions, woody debris, and hydraulic characteristics (Table 2).

Landscape characterization

Land use – land cover data and patch heterogeneity (a measure of landscape fragmentation) reflect the extent of human intervention in shaping the landscape and are collectively referred to as land-use factors. Landscape factors that are fixed by geologic and topographic influences are considered separately and are referred to collectively as geology–structure variables. These landscape factors were surficial geology, catchment area, mean catchment slope, and standard deviation of catchment elevation.

Land-use patterns for the study area were derived from existing digital data obtained from the Michigan Department of Natural Resources (Michigan Resource Information System data base) and were based on aerial photography from the late 1970s. Mapping resolution for these data is approximately 1 ha, with a minimum lateral dimension of 61 m. A visual comparison of the digital data to late 1980s photographs revealed that the 1970s digital data were about 90% accurate over the Flint Basin. The majority of observed land use changes reflect wetland habitat loss near urban centers. The classification of

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Fig. 1. Location of the study sites and six river basins in the Saginaw River Drainage.

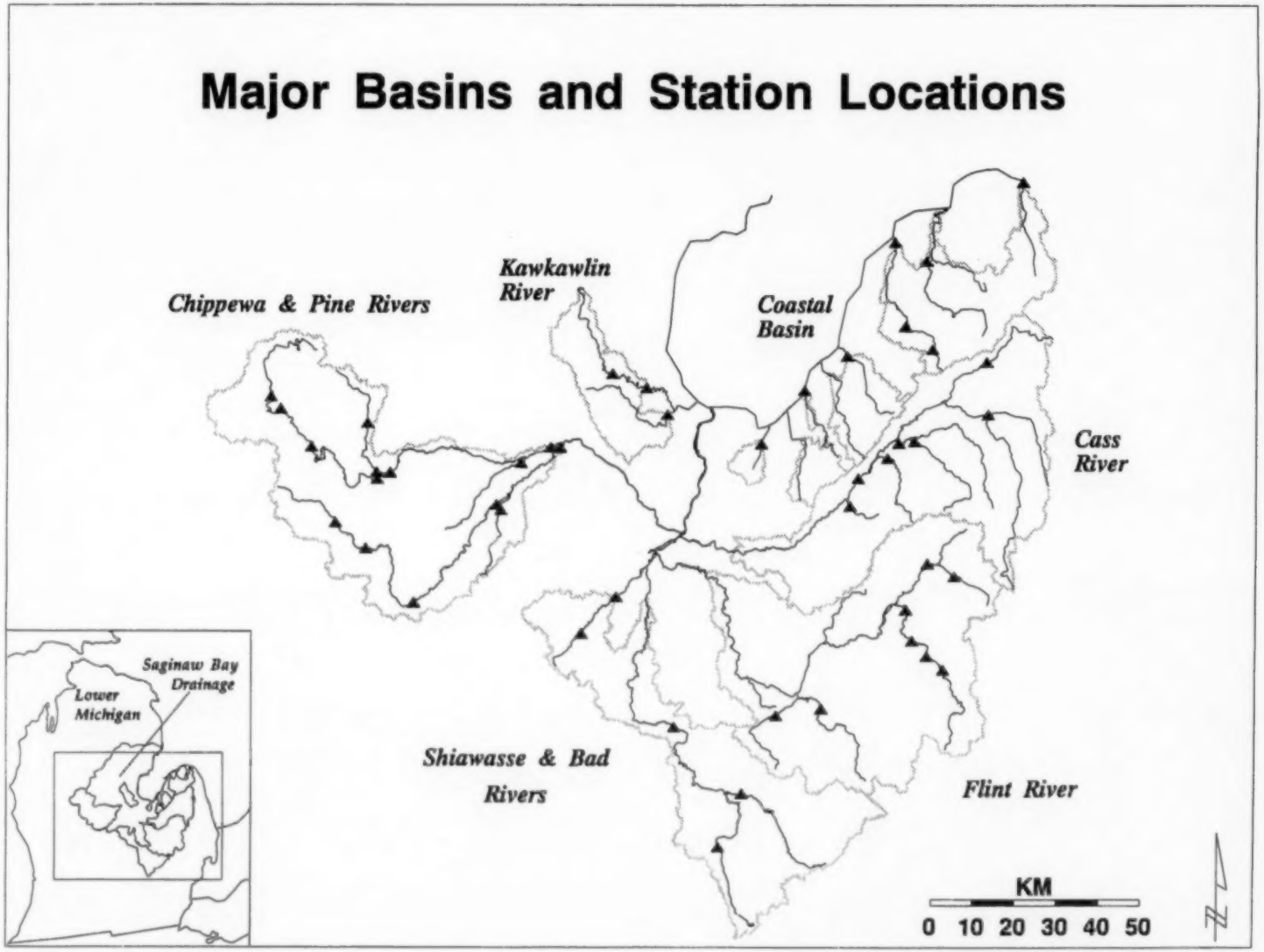

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Table 1. Variables used to describe macroinvertebrate communities at the sites.

Metric	Attribute
Richness	Total no. of macroinvertebrate taxa (genera)
EPT richness	Total no. of Ephemeroptera, Plecoptera, and Trichoptera taxa (genera)
Total abundance	Total no. of macroinvertebrates
Dominant 2 taxa	Proportion of the total nos. of individuals accounted for by the two most abundant taxa at a site
Erosional taxa	Proportion of the total nos. of individuals that are exclusively found in erosional habitats
Depositional taxa	Proportion of the total nos. of individuals that are exclusively found in depositional habitats
HBI	Hilsenhoff's Improved Biotic Index (Hilsenhoff 1987), which assesses tolerance to low oxygen
Chironomidae	Proportion of the total nos. of individuals that are Chironomidae
Detritivores	Proportion of total nos. of individuals that are detritivores
Omnivores	Proportion of total nos. of individuals that are omnivores
Predators	Proportion of total nos. of individuals that are predators
Shredders	Proportion of total nos. of individuals that are shredders (large organic particle feeders)
Gatherers	Proportion of total nos. of individuals that are gatherers (small organic particle feeders)
Filterers	Proportion of total nos. of individuals that are filterers (filter small organic particles)
Grazers	Proportion of total nos. of individuals that are grazers (scrape algae and other material from rock surfaces)

Note: Unless otherwise noted, Merrit and Cummins (1984) was used to designate categories.

Table 2. Reach-scale habitat variables measured at, or calculated for, each study reach.

Variable	Methods
% shallows (shallow)	Visual estimate of the percentage of wetted area less than 10 cm in depth
% deep pools (deep)	Visual estimate of the percentage of wetted area as pools > 0.5 m in depth
Maximum depth	Depth (m) of deepest part of stream reach
Bankfull width (BFW)	Average width (m) of stream channel at bank full discharge calculated from three transects
Bankfull depth (BFD)	Average depth (m) of stream at bank full discharge calculated from three transects
Flood ratio	Proportion of flood depth represented by summer low flow
Mannings's *N*	An estimate of channel roughness or flow resistance (Chow 1959)
Stream power (power)	Power per unit width (Petts and Foster 1985)
% fines (fine)	Proportion of erosional substrates less than 2 mm in diameter measured volumetrically from grab samples (Platts et al. 1983)
Woody debris (wood)	Length (m) of large woody debris (> 10 cm diameter) per 100 m of stream channel
% macrophyte cover	Visual estimate of the percentage of total wetted area covered by aquatic macrophytes
% canopy	Visual estimate of the percentage of wetted area shaded by shrub or tree canopy
% eroded banks (eroded)	Visual estimate of the percentage of banks that were washed or sloughing (Platts et al. 1983)

land use – land cover categories was based on a modified version of the Anderson et al. (1976) scheme, which was constructed specifically for natural resource applications. Based on both areal extents of certain land use classes and results of preliminary statistical analyses, we aggregated land use categories into nine categories: urban, row-crop agriculture, non-row-crop agriculture, mixed forest, deciduous forest, herbaceous range land, shrubby range land, nonforested wetlands, and forested wetlands. Non-row-crop agriculture in this region is largely represented by orchards with occasional feedlots, and range lands are predominantly abandoned fields. In this study, we report and analyze land use – land cover values as the percentage of total catchment area (or the percentage of stream buffer area contained within each catchment; see Methods below).

Quaternary geology data were digitized from Farrand and Bell (1984) at a scale of 1:500 000 and were reported as a proportion of the total catchment area. Based on areal extents of minor categories and preliminary statistical analyses, some geological categories were combined or deleted altogether. The geological variables used in the analyses were outwash sand and gravel; dune–lacustrine sand; peat–muck; lacustrine clay; and fine, medium, and coarse till.

For each sampling station, we used U.S. Geological Survey (USGS) topographic maps (1:24 000) to manually delineate the catchment boundaries, which were digitized using ARC/INFO. Stream data were derived from digital line graph data at a scale of 1:100 000 (USGS). Patch density was calculated from land use – land cover maps as the number of patches per square kilometer. Elevation and slope for the whole catchment were obtained from 1° digital elevation models (USGS) at a scale of approximately 1:250 000. We used the standard deviation in elevation to represent topographic heterogeneity. Valley slope was derived from elevation data using ARC/INFO algorithms. We calculated slope for the buffer data (see explanation below) from 30" digital elevation models at a scale of 1:100 000. All data bases were transformed into a common digital format, projected onto a common coordinate system (Albers), and analyzed in ARC/INFO as vectors.

We used buffer analysis to extract landscape data for a region 100 m on each side of the river (Richards and Host 1994). We used this buffer distance because a variety of stream functions respond to riparian features within this distance from the stream (see Large and Petts 1994) and because of the minimum width of the land-cover data (61 m). This procedure allowed us to compare landscape descriptors within the river corridor with data derived for whole catchment. We

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performed identical analyses on both the buffer and whole catchment data to determine interrelationships between macroinvertebrates, physical habitat, and landscapes.

Statistical analysis

Using redundancy analysis (RDA; a canonical extension of principal component analysis) we examined relationships among the individual multivariate data sets. RDA is a form of direct gradient analysis (ter Braak and Prentice 1988) that describes variation between two multivariate data sets. Specifically, a matrix of predictor variables (e.g., stream habitat variables) is used to quantify variation in a matrix of response variables (e.g., a community matrix). In RDA, the site scores from a principal component analysis (PCA) are regressed iteratively against a set of environmental variables, and the fitted values of the regression become new site scores (Jongman et al. 1987). The PCA is thus constrained by the environmental or predictor variables. RDAs were performed using the program CANOCO (ter Braak 1991*a*, 1991*b*). Two important outputs from this method are (*i*) the interset correlations of environmental variables with the RDA axes, which identify environmental variables that have strongest influence on the ordination, and (*ii*) the fraction of total variance for each predicted variable explained by the RDA axes (Jongman et al. 1987). In RDA, the explained variance is derived from the sum of squares of regression (ter Braak 1991*a*).

In this study, we conducted two sets of RDAs. In the first set, we quantified variation in the macroinvertebrate community data as a function of the stream habitat variables. We used this information to select the most important habitat variables. In the second set of RDAs, we attempted to quantify variation in this reduced stream habitat data matrix as a function of land use or geologic variables. We were thus able to use these RDAs to develop explanatory linkages among data sets at different scales: landscape to the stream reach and stream reach to macroinvertebrate community.

To reduce the number of habitat variables, we selected those variables that had the strongest influence on the macroinvertebrate assemblage. Habitat variables that had correlations of 0.3 or greater with one of the first three species axes of the RDA were retained for further analysis. We then examined the ability of the landscape data to predict variation in the reduced set of habitat variables.

We used partial RDA to determine the relative influences of land use and geology–structure landscape variables on physical habitat and macroinvertebrate assemblages. In the partial RDA process, one of the landscape variable types is held constant and variation due to the other landscape set is examined independently (Borcard et al.1992). With this method, total variation in a multivariate data set is decomposed in a manner analogous to analysis of variance (ter Braak 1991*b*). For this analysis, we separated variation in habitat variables into four categories: (*i*) variation explained by land use variables independently of geology–structure variables; (*ii*) variation explained by geology–structure variables independently of land use variables; (*iii*) variation shared by both geology–structure and land use variables (this shared variation can be due to the dependance of one type of variable on the other, e.g., the types of soil found in a catchment will largely determine the types of agriculture that can be practiced); and (*iv*) variation not accounted for by land use or geology–structure.

In all cases, we used Monte Carlo permutation tests to determine the statistical validity of the associations between the various multivariate data sets. These tests were conducted by randomly permuting the sample numbers within the environmental variables. The environmental variables (or predictor variables) were then randomly linked with the species (or predicted variable) data, and a new ordination was calculated. This procedure was repeated 100 times to develop a population of eigenvalues. If the species variables respond to the environmental variables, then the test statistic calculated from the observed data will be larger than the data derived from most of the random simulations. An association was considered significant if the observed eigenvalue was within the five largest simulated values ($p < 0.05$).

Results

Landscape characteristics

Individual catchments ranged from 14 to 99% in total agricultural land use, with the Coastal Basin catchments exhibiting the greatest and the Kawkawlin Basin catchments having the lowest proportions of agricultural land use (Table 3). The Chippewa–Pine and Kawkawlin basins exhibited the greatest diversity of land use and cover types within the study region. Wetlands represented a minor land use component, with individual catchments ranging between 0 and 15% land area. The Kawkawlin and Cass basins had the greatest proportion of wetlands, each having a median of 7%. Patch density, a measure of landscape dissection with respect to land use or cover, was low in the Coastal Basin (245 patches/km^2), intermediate for the Cass, Shiawassee, and Chippewa–Pine basins, and highest in the Flint catchment (1067 patches/km^2). Patch density was highly negatively correlated with agricultural and forest land use and highly positively correlated with urban land use.

The mean catchment area varied greatly among the basins, ranging from 15 000 ha in the Coastal Basin to over 50 000 ha in the Chippewa–Pine (Table 3). The standard deviation of elevation, a measure of topographic complexity, also showed large variations, ranging from less than 10 m in the Cass and Kawkawlin to over 30 m in the Shiawassee and Chippewa–Pine basins.

Similar to land use, there was a wide range in variation among the dominant geomorphic features of the individual catchments. The Coastal and Kawkawlin basins were dominated by lacustrine clays and dune and lacustrine sands; together, these geomorphic features accounted for over 75% of the land area of individual catchments (Table 4). The Cass and Shiawassee basins were dominated by medium tills, while the Flint and Chippewa–Pine basins were dominated by coarse tills. The Cass, Flint, and Chippewa–Pine basins also had relatively high proportions of outwash sand and gravel. In most cases, however, there was a high degree of variation in geomorphology among catchments within each basin.

Physical habitat characteristics

Habitat variables also exhibited considerable variation within the major basins (Table 5). Both percent shallow and percent deep habitats were greatest at the Coastal and Kawkawlin basins while the Coastal Basin also displayed the highest bankfull width and erosion. Kawkawlin Basin sites were almost completely dominated by fine substrates. Overall, the maximum depth was less that 1 m. The Kawkawlin and Shiawasse basins had at least twice as much woody debris as the other basins. Stream power was also lowest at the Kawkawlin and Shiawassee sites. The proportion of canopy cover was highest in the Shiawassee and Cass basins; however, considerable variation in canopy cover was observed in all basins.

Macroinvertebrate characteristics

Among the six basins, we observed considerable variation in the macroinvertebrate assemblage variables during summer (Table 6). In particular, sites within the Kawkawlin differed

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Table 3. Median and quartiles of landscape variables used to describe geology and structure of the study catchments.

	Coastal Basin ($n = 8$)*	Cass ($n = 7$)	Flint ($n = 8$)	Shiawassee ($n = 5$)	Chippewa–Pine ($n = 15$)	Kawkawlin ($n = 3$)
Peat–muck	0	0	0	0	0	0
	0–0	0–2	0–0	0–0	0–0	0–0
Lacustrine clays	57	0	10	0	0	26
	15–60	0–0	2–30	0–0	0–6	21–26
Dune – lacustrine sands	26	18	0	0	0	57
	14–43	6–33	0–0	0–72	0–1	46–59
Outwash sand and gravel	0	22	19	0	24	0
	0–0	10–36	16–29	0–19	18–32	0–0
Fine tills	4	0	0	3	0	21
	0–22	0–0	0–0	0–11	0–1	19–30
Medium tills	14	46	5	48	4	0
	0–27	34–47	3–34	1–66	0–19	0–0
Coarse tills	0	10	48	13	50	0
	0–0	1–20	28–53	0–27	23–66	0–0
Slope (degrees)	0.17	0.23	0.44	0.30	0.38	0.16
	0.10–0.20	0.22–0.35	0.37–0.47	0.19–0.31	0.32–0.40	0.13–0.16
Elevation (m)	212	240	283	279	279	207
	188–223	219–242	256–291	202–284	262–301	200–209
Elevation SD	35	43	77	37	64	30
	10–56	32–51	38–97	32–69	53–89	27–33
Catchment area (ha $\times 10^2$)	153	166	224	331	393	223
	45–231	106–292	126–471	129–487	186–852	203–242

*n, number of catchments in each basin.

Table 4. Summary of landscape variables in six major basins of the Saginaw drainage.

	Coastal Basin ($n = 8$)*	Cass ($n = 7$)	Flint ($n = 8$)	Shiawassee ($n = 5$)	Chippewa–Pine ($n = 15$)	Kawkawlin ($n = 3$)
Agricultural land	0	1	3	0	4	2
	0–0	1–1	2–3	0–1	2–6	1–2
Row crops	86	58	38	44	48	26
	82–96	51–66	36–61	34–59	30–56	22–51
Urban	1	2	9		10	2
	0–1	1–2	4–12	3–11	1–3	1–4
Deciduous forest	6	17	18	19	23	57
	3–9	15–21	14–19	17–21	20–34	35–61
Mixed hardwood	0	0	3	1	5	0
	0–0	0–1	1–3	1–1	4–6	0–0
Range: herb	1	7	13	13	7	3
	1–1	5–11	7–14	1–16	4–8	2–3
Range: shrub	1	5	7	7	6	3
	0–2	4–6	3–8	3–9	5–7	3–3
Forested wetlands	0	0	2	1	1	2
	0–0	0–0	1–3	0–2	0–1	1–2
Nonforested wetlands	2	7	4	4	4	5
	0–3	4–8	3–5	3–4	3–6	3–5
Patch density (no./km^2)	245	657	1067	773	764	578
	167–336	514–890	772–1121	543–916	628–835	460–608

Note: Values are reported as median and quartiles. Land use–cover represent percent areas of each catchment. Agricultural land refers to farming practices other than row crops.

*n, number of catchments in each basin.

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Table 5. Medians and quartiles of reach-scale physical habitat variables by major basins.

	Coastal Basin ($n = 8$)*	Cass ($n = 7$)	Flint ($n = 8$)	Shiawassee ($n = 5$)	Chippewa–Pine ($n = 15$)	Kawkawlin ($n = 3$)
Shallow	45	5	5	10	5	10
	1–60	3–8	0–10	5–20	2–10	10–25
Deep	18	5	10	5	10	50
	0–60	0–10	0–18	1–15	0–18	30–55
Maximum depth	0.68	0.64	0.96	0.67	0.76	0.70
	0.55–0.79	0.60–0.95	0.84–1.20	0.49–1.00	0.62–1.17	0.66–0.85
BFW	19.1	11.9	11.2	9.1	18.6	12.6
	11.9–23.9	11.2–15.7	8.2–14.6	7.9–14.9	12.2–28.3	10.1–19.0
BFD	1.16	0.61	0.80	0.81	0.93	0.70
	0.78–1.45	0.54–1.21	0.72–0.94	0.78–0.92	0.70–1.38	0.65–0.74
Flood ratio	14.2	13.9	24.6	23.6	29.6	19.9
	6.0–19.5	12.4–19.6	21.7–36.4	16.1–31.9	18.9–32.5	19.1–20.5
Manning's *N*	0.09	0.07	0.07	0.08	0.09	0.10
	0.06–0.10	0.06–0.11	0.05–0.10	0.08–0.11	0.07–0.11	0.08–0.11
Power	1.0	2.2	2.7	0.4	0.9	0.5
	0.8–2.0	1.8–3.9	0.4–5.0	0.2–0.4	0.7–2.6	0.3–0.6
Fine	48	28	54	71	24	100
	37–84	24–30	32–100	60–100	17–40	97–100
Wood	17	6	12	40	10	88
	2–43	1–29	1–55	14–63	7–24	44–146
Macrophytes	0	0	2	1	5	0
	0–1	0–6	0–3	0–5	1–30	0–5
Canopy	30	40	20	40	10	35
	0–45	10–55	6–55	40–50	3–30	17–57
Eroded	65	10	30	20	25	40
	15–85	8–33	20–48	15–85	6–45	21–50

*n, number of catchments sampled in each basin.

considerably from the other basins; the Kawkawlin was notable for the high proportion of shredders and filterers and the low proportion of detritivores and gatherers. In contrast to the other major basins, both the Coastal and Kawkawlin basins had lower proportions of strictly erosional taxa and higher proportions of depositional taxa. Taxa from the Coastal and Kawkawlin basins also exhibited higher median values for Hilsenhoff's Biotic Index (HBI; Hilsenhoff 1987); this suggests that taxa at these sites tolerate lower oxygen concentrations than those in other major basins. These basins also had the lowest Ephemeroptera–Plecoptera–Tricoptera (EPT) species richness. Total species richness was highest in the Chippewa–Pine Basin and lowest within the Coastal Basin. Ranges of total abundance of macroinvertebrates were large in all basins except the Shiawassee.

In general, patterns of macroinvertebrate assemblage variables in autumn (Table 7) were similar to those observed during summer. The Kawkawlin and Coastal basins had high HBI scores, low EPT scores, low proportions of erosional taxa, and high proportions of depositional taxa. The proportion of predators was exceptionally high in the Kawkawlin Basin because of the abundance and trophic classification of one chironomid genus. Total numbers of macroinvertebrate were highest in the Kawkawlin.

Physical habitat – macroinvertebrate relationships

Physical habitat variables explained a total of 37% of the macroinvertebrate data in summer and 46% in fall. In summer the first RDA axis was correlated most strongly with canopy extent and percent deep (Table 8). The numbers of depositional taxa and the proportion of shredders increased with canopy extent and percent deep. The average low oxygen tolerance (increasing HBI) also increased with canopy extent and percent deep. The proportion of detritivores, number of erosional taxa, and numbers of EPT taxa decreased with increasing canopy and percent deep water. The second axis was defined by physical characteristics related to stream size including bankfull width and bankfull depth as well a decrease in canopy coverage attributable to increases in stream width (Table 8). These size-related factors had the greatest influence on the proportion of filterers and gatherers in the assemblage. The third axis was defined by factors relating to stream hydraulics and depths. These factors had the greatest influence on percent dominance.

The macroinvertebrate patterns observed in autumn were similar to those observed in the summer. Erosional and depositional taxa, EPT taxa, HBI, and detritivore abundance were explained by percent deep, percent fines, and woody debris (Table 9). Macroinvertebrate assemblage characteristics reflected the change along this axis from shallower reaches, with low proportions of fines and woody debris, to reaches with a high percentage of fines, pools, and large amounts of woody debris. Many of the changes in macroinvertebrate assemblage metrics along this axis were related to habitat preference, i.e., whether taxa favored erosional or depositional environments. Increasing numbers of depositional taxa were associated with

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Table 6. Median and quartiles of macroinvertebrate community characteristics in summer for six major basins of the Saginaw drainage.

	Coastal Basin ($n = 8$)*	Cass ($n = 7$)	Flint ($n = 8$)	Shiawassee ($n = 5$)	Chippewa–Pine ($n = 15$)	Kawkawlin ($n = 3$)
Chironomidae	73	63	48	27	53	66
	31–82	43–65	25–67	21–30	11–68	57–76
Omnivores	23	20	12	14	17	15
	5–31	18–20	9–25	12–17	13–24	13–28
Detritivores	63	67	77	81	75	21
	34–82	65–72	67–87	75–85	70–84	14–40
Shredders	19	20	10	7	7	43
	8–45	15–21	7–14	4–7	5–15	36–62
Gatherers	73	65	62	64	66	43
	37–80	51–75	58–63	60–68	56–80	26–56
Filterers	9	14	28	13	13	21
	4–48	9–31	8–33	13–31	9–28	19–51
Grazers	23	12	19	38	26	27
	4–56	8–20	9–44	35–39	13–53	14–37
Predators	1	1	1	1	1	2
	0–2	0–2	0–2	0–2	1–2	1–2
Two dominant species	66	54	48	55	50	61
	42–86	50–61	41–60	50–60	47–61	49–71
Total abundance	302	483	332	321	418	587
	96–728	339–669	183–764	312–379	323–656	339–604
HBI	6.4	5.6	5.6	6.2	5.2	7.8
	6.2–7.8	5.5–5.8	5.4–6.2	5.7–6.4	4–5.8	7.6–8.4
Erosional taxa	19	33	42	50	42	8
	11–62	27–48	30–60	42–67	15–71	7–25
Depositional taxa	57	12	22	28	7	58
	23–73	7–16	8–33	15–36	6–20	51–72
Species richness	18	22	21	21	27	21
	15–21	16–23	17–29	16–23	24–28	21–25
EPT taxa richness	5	7	7	7	11	3
	3–8	6–8	5–10	6–10	7–13	3–4

*n, number of catchments that were sampled in each basin.

increased depth, percent fines, and woody debris; EPT taxa decreased with these habitat factors since many of these taxa are associated with erosional substrates. HBI increased along the first axis, indicating increased tolerance to low oxygen with increasing depositional taxa. The second axis was related to stream size (canopy cover, bankfull width) and stream bank erosion. Shredders increased proportionally with increasing canopy coverage, and total macroinvertebrate abundance increased with increasing stream width. The third axis was most closely related to shallows, which had the greatest influence on filterers.

Landscape – physical habitat relationships

RDA showed that approximately 50% of the variation in physical habitat variables was explained by the landscape data. Geology–structure data accounted for 22% of the variation in physical habitat variables and land use data accounted for 16%. However, only geology–structure variables had a significant partial RDA. Shared variation due to both geology–structure and land use data accounted for 11% of the total variation. These analyses suggest that geomorphic variables were most consistent in describing variation in physical habitat.

We found considerable differences in the amounts of variation in individual habitat variables explained by geology–structure and land-use data (Fig. 2). In addition, the relative contributions of geology–structure and land use with respect to explaining individual habitat variables were different. For example, bankfull width, bankfull depth, flood ratio, and shallows had over 60% of their variance described, while percent deep water, bank erosion, and maximum depth had less than 30% of their variance described by the landscape data (Fig. 2). Bankfull width was most strongly influenced by geology–structure variables and only minimally by land use. In contrast, amount of woody debris was most influenced by land-use data and only minimally by geology–structure. Other variables such as bankfull depth, canopy cover, and shallows were influenced more or less evenly by both sets of landscape data. Flood ratio was also influenced evenly by geology–structure and land use, and the shared influence of these factors.

The RDA was also used to assess the influence of specific landscape variables within the geology–structure and land use data sets. The most influential of the geology–structure landscape variables were catchment area and standard deviation (SD) of elevation (Fig. 3*a*). Geologic variables had the strongest influence on physical habitat parameters related to channel cross sectional diameter (e.g., bankfull width and bankfull depth). In addition, these variables demonstrated that the control of physical habitat is largely determined by landscape

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Table 7. Medians and quartiles of macroinvertebrate community characteristics in fall for six major basins of the Saginaw River drainage.

	Coast Basin ($n = 8$)*	Cass ($n = 7$)	Flint ($n = 8$)	Shiawassee ($n = 5$)	Chippewa–Pine ($n = 15$)	Kawkawlin ($n = 3$)
Chironomidae	58	59	25	58	37	74
	21–91	45–67	19–49	51–61	16–53	58–80
Omnivores	20	10	13	14	11	2
	6–28	9–18	7–21	13–23	5–17	2–3
Detritivores	70	67	79	80	78	14
	33–79	61–76	73–86	74–85	74–84	11–16
Shredders	14	23	10	9	10	3
	6–38	14–27	6–14	6–15	7–19	2–4
Gatherers	72	62	60	62	81	10
	30–82	53–85	55–65	60–67	62–86	6–11
Filterers	3	31	36	6	10	4
	1–38	6–42	20–38	2–9	5–29	3–5
Grazers	12	7	34	19	24	10
	5–47	5–12	15–46	17–21	13–37	5–28
Predators	1	0	0	2	1	73
	0–4	0–1	0–1	1–4	0–2	56–80
Two dominant species	59	49	55	44	50	74
	48–72	45–51	50–62	41–48	42–53	71–81
Total abundance	151	326	682	499	760	901
	145–422	227–732	349–756	480–838	349–1046	754–2700
HBI	6.7	5.3	5.7	6.1	4.3	7.8
	6–7.8	4.9–5.8	4.7–6.3	5.3–6.2	3.9–4.9	7.8–7.8
Erosional taxa	17	32	52	20	52	6
	2–40	25–46	28–76	19–24	30–65	5–7
Depositional taxa	42	16	17	48	13	85
	29–61	12–21	5–25	28–50	7–32	66–86
Species richness	19	22	22	30	27	23
	15–22	19–24	20–25	20–32	24–31	22–24
EPT taxa richness	3	6	8	7	9	2
	1–6	6–7	6–9	7–11	7–13	2–3

*n, number of catchments that were sampled in each basin.

Table 8. Results of redundancy analysis (RDA) of the influence of physical habitat variables on summer macroinvertebrate assemblage characteristics.

	RDA1	r	RDA2	r	RDA3	r
Habitat variables	Canopy	0.75	BFW	0.52	Flood ratio	–0.41
	% deep	0.50	Canopy	–0.47	Maximum depth	–0.39
			BFD	0.32	% shallow	0.32
Invertebrates	Depositonal taxa (+)	32.4	Filterer (+)	37.8	Dominance (+)	18.8
	Shredder (+)	29.4	Gatherer (–)	24.1		
	Detritivore (–)	27.7				
	HBI (+)	27.0				
	EPT (–)	25.4				
	Erosional taxa (–)	22.3				

Note: The habitat variables listed had correlations (r) with the first three axes >0.30. The dominant invertebrate variables on each of the RDA axes are shown. Invertebrate values indicate the proportion of variance explained in the variable. The plus and minus signs in parentheses indicate the direction of invertebrate responses to the RDA axis.

characteristics at larger spatial scales. Increasing channel dimensions are associated with increasing catchment area (Richards 1982). In addition, channel dimension, particularly bankfull depth, strongly influences canopy cover since the extent of canopy coverage decreases as stream width increases.

In our landscape analysis, slope and lacustrine clay were important predictors on RDA axis 2 and had the strongest influence on the flood ratio (Fig. 3*a*). Slope is a fundamental parameter for predicting the rates of water flow across surfaces. Lacustrine clay soils are relatively impermeable to water as compared with more porous surface materials such as sand

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Fig. 2. Results of variance decomposition from partial redundancy analysis (RDA) indicating percent variance in physical habitat variables explained by land use (LU), geology and structure variables (GEO/STR), shared variation between the two landscape data sets (SHARED), and unexplained variation (UNEXPL).

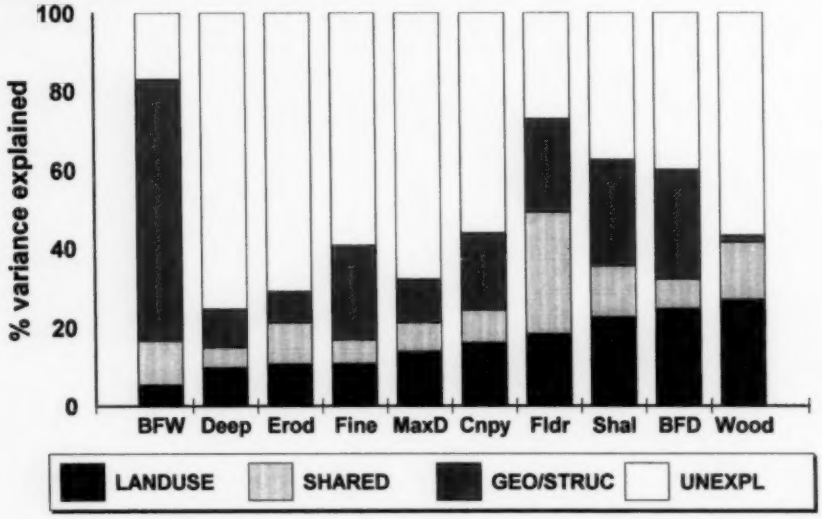

Table 9. Results of redundancy analysis (RDA) of the influence of physical habitat variables on fall macroinvertebrate assemblage characteristics.

	RDA1	*r*	RDA2	*r*	RDA3	*r*
Habitat variables	% deep	0.54	Canopy	−0.42	% shallows	−0.38
	% fines	0.47	BFW	0.36		
	Wood	0.34	Erosion	−0.31		
Invertebrates	Erosional taxa (−)	55.1	Total abundance (+)	39.3	Filterer (+)	18.8
	Depositional taxa (+)	50.5	Shredder (−)	25.5		
	Detritivore (−)	33.8				
	EPT (−)	29.5				
	Predator (+)	27.8				
	HBI (+)	26.6				

Note: The habitat variables listed had correlations (*r*) with the first three axes >0.30. The dominant invertebrate variables on each of the RDA axes are shown. Invertebrate values indicate the proportion of variance explained in the variable. The plus and minus signs in parentheses indicate the direction of invertebrate responses to the RDA axis.

or gravel. The geology–structure variables outwash sand and gravel and medium till (RDA axis 3) had the greatest influence on fines and shallows (Fig. 3*a*). In the presence of sandy parent materials, larger proportions of sand were found in the stream channel and a larger proportion of the stream reach was shallow.

The partial RDA (Fig. 3*b*), which shows the unique contributions of geology–structure variables in the absence of land-use variables, indicates the importance of catchment area and the two major geologic areas in the region: ancient lakebed (lacustrine clays) or glacial outwash. Variation attributable to catchment area and SD elevation was unique to the geology–structure variables. Variation attributable to slope, however, was shared between the two landscape data sets.

The most important land-use variables on the first axis were shrub, non-row-crop agriculture, and patch density (Fig. 4*a*); all variables were originally correlated with row-crop agriculture. These variables had strongest influence on flood ratio, shallows, and woody debris (Fig. 4*a*). In general, shrubs and non-row-crop agriculture are associated with permanent vegetation and influence the rate of water and nutrient movement across surfaces. In our study, higher values of patch density were associated with non-row-crop agriculture and may also indicate decreased runoff potential. The link between increasing permanent vegetation and the presence of woody debris in the stream is obvious. A portion of the variance for canopy cover was described by this axis and most likely indicates the portion of variance attributable to streamside vegetation. Maximum depth, erosion, and fines also had a considerable portion of their variance described by permanent vegetation and patch density. The presence of fines in the stream channel may be related to the extent of permanent ground cover. The influence of permanent vegetation and patch density on maximum depth and eroding banks is less obvious; however, erod-

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Fig. 3. Percent variance of physical habitat variables explained by geology and structure (GEO/STR) landscape variables. Legends indicate GEO/STR variables that had correlations (r) greater than 0.3 with the RDA axes. (a) Full redundancy analysis. (b) Partial redundancy analysis using land use variables as covariates.

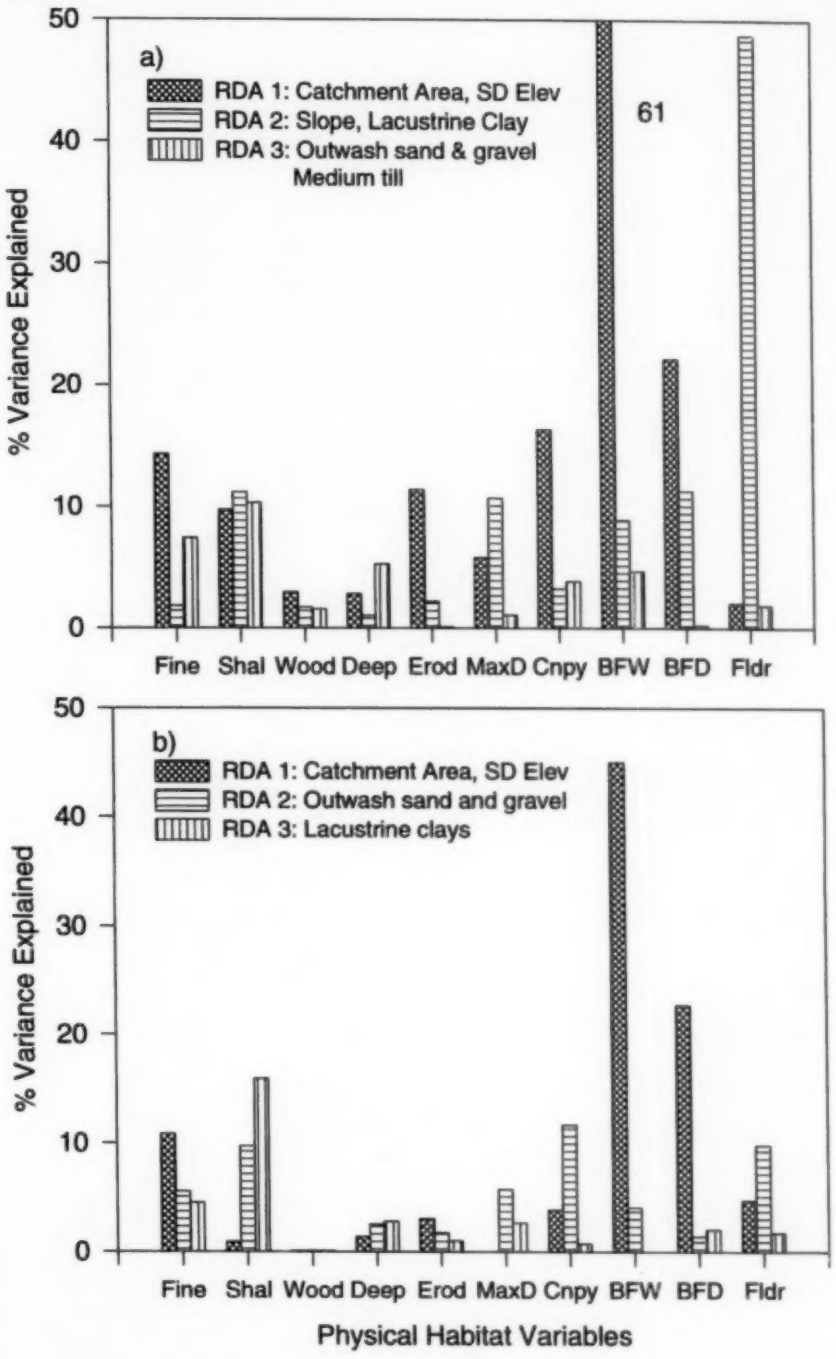

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Fig. 4. Percent variance of physical habitat variables explained by land use landscape variables. Legends indicate land use variables that had correlations (r) greater than 0.3 with the RDA axes. (a) Full redundancy analysis. (b) Partial redundancy analysis using land use variables as covariates.

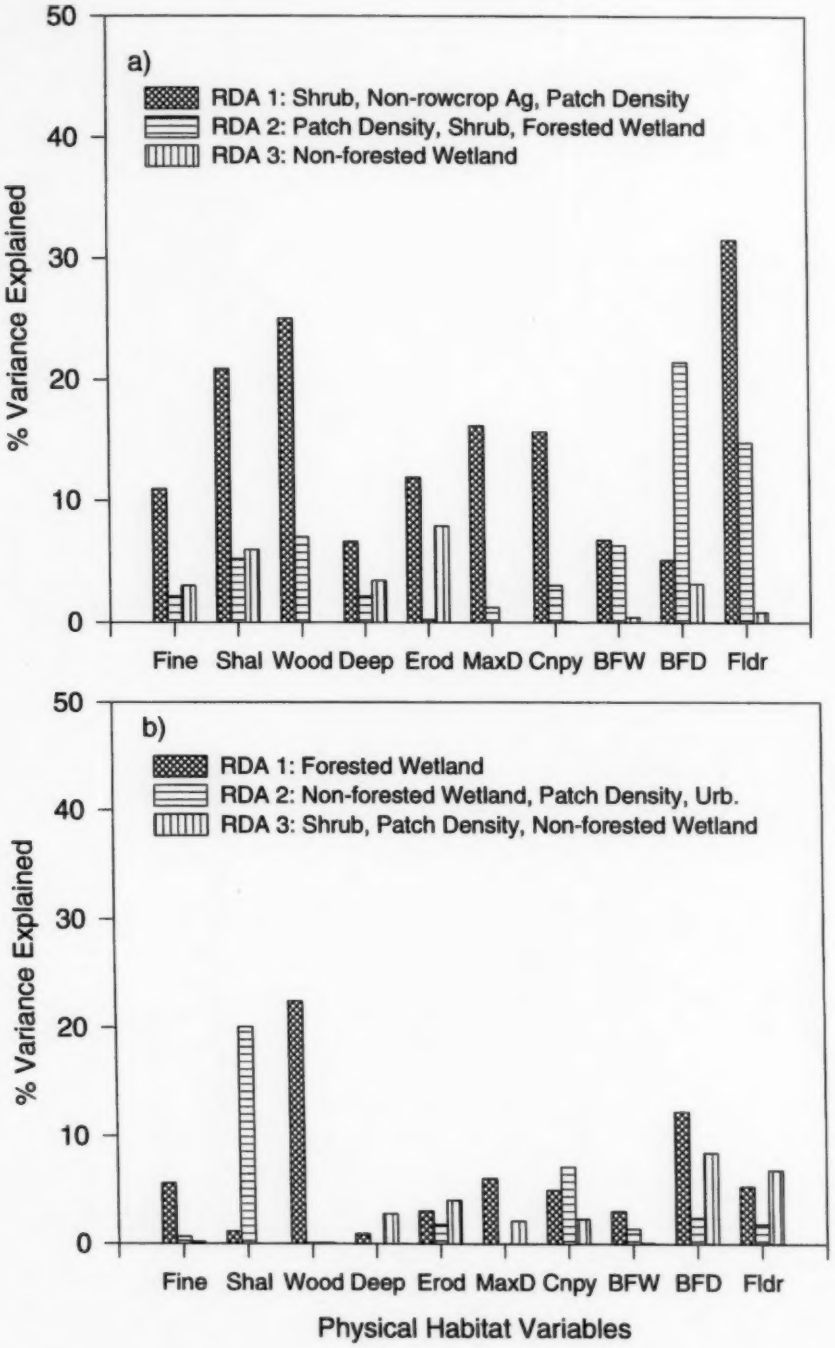

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Table 10. Percent total variance explained in physical habitat variables by full catchment and stream buffered landscape variables in the redundancy analysis.

	Catchment	Stream buffer
BFW	83.1	83.4
Flood ratio	72.9	64.0
Fines	40.8	60.0
Shallows	62.7	58.8
Wood	43.5	48.0
BFD	60.1	46.5
Canopy	44.0	42.1
Eroded	29.2	37.2
Maximum depth	32.2	25.1
Deep pool	24.5	23.9
All variables	49.3	48.9

Note: Both sets of landscape variables had significant relationships to the habitat variables ($p < 0.05$).

ing banks are frequently associated with streams of intensively agricultural regions (Menzel et al. 1984). The proportion of forested and nonforested wetlands accounted for additional variance in bankfull depth and flood ratio.

The partial RDA of land use variables in our study (Fig. 4*b*) emphasized the unique contribution of wetlands to instream habitat characteristics. The wetland categories appeared on all three of the partial RDA axes and contributed to the explained variation of several of the physical habitat variables, particularly wood, bankfull depth, shallows, and flood ratio.

Whole catchment versus stream buffer comparisons

Surprisingly, there was little difference (<5%) in the total amount of variance in physical habitat parameters that could be described by the buffer versus the whole catchment data (Table 10). Only percent fines and percent erosion had more variation (>5%) explained by the stream buffer data. These results suggest that landscape elements lateral to the stream channel have a modifying influence on both sediment delivery and reach-scale erosional processes. However, some channel variables were more influenced by whole catchment variables. For example, maximum depth, bankfull depth, and flood ratio had more variation explained by the catchment data than the stream buffer data. Since hydrology is dependent on channel and other flow-related variables, and these variables are regulated at the catchment scale, stream buffer data were not as predictive as whole catchment variables.

Discussion

Our results suggest that major patterns in macroinvertebrate assemblages across large heterogenous landscapes are largely regulated by habitat and morphological features of streams. Through their influence on stream morphometry, surficial geology, and land-use patterns strongly influenced variation in macroinvertebrate assemblage structure among the basins studied. The Kawkawlin and Coastal basins represented the extremes of these relationships. Catchments within the Kawkawlin and Coastal basins were dominated by clay and sandy soils and relatively flat topography. Consequently, macroinvertebrate assemblages had a low proportion of erosional macroinvertebrate taxa and were dominated by taxa tolerant to oxygen depletion. Coastal Basin catchments, however, had a high (>85%) percentage of row-crop agriculture, whereas Kawkawlin catchments had more diverse land covers, including forested wetlands that contributed to high amounts of woody debris. The low species richness at the Coastal Basin sites probably results from degraded habitat commonly associated with row-crop agriculture (see also Lenat 1984). Species richness in Kawkawlin streams, which had large amounts of woody debris and more heterogenous habitats, was as high or higher than other basins. Beyond these contrasts, the direct influence of geology–structure and land use on habitat and macroinvertebrate assemblages among basins was more difficult to quantify because of the large amount of variation at this scale.

When viewed at the smaller catchment scale, geology–structure and land use factors had similar magnitudes of influence on macroinvertebrate assemblages. Effects on the biological community were mediated through the physical habitat. The mechanisms of influence were different, however, between the land use and geology–structure data. Geomorphic variables, particularly catchment area, had the most distinct influence on macroinvertebrate assemblage structure, largely through its influence on the cross-sectional area of the channel. Even in the relatively narrow range of stream sizes observed in this study (second to fourth order), differences in macroinvertebrate assemblages attributable to increasing stream width were observed. In particular, functional feeding groups were more influenced by catchment area than any other landscape variables, through the influence on channel dimension. These observations are consistent with expectations of stream continuum theory (Vannote et al. 1980), which predicts longitudinal changes in assemblage structure resulting from the decreasing influence of riparian zones and other physical gradients that occur with increasing stream size.

Surficial geology had a different influence than catchment area. For example, while catchment area influenced dimensional profiles of stream channels, landform type had a strong influence on substrate type and canopy extent and composition. The presence of erosional or depositional taxa was due in part to the relative proportions of lacustrine clays and outwash sands. Substrate composition strongly influences macroinvertebrate assemblage patterns in the Saginaw Bay drainage (Richards et al. 1993) and can have a profound effect on many invertebrate distributions (Minshall 1984). Canopy characteristics can have a strong influence on shredders and detritivores by altering the quality and abundance of detrital inputs associated with canopy coverage (Egglishaw 1964; Molles 1982; Corkum 1992).

The relative abundances of lacustrine clay, outwash sands, and morainal tills also influences hydrologic and temperature patterns. Outwash areas typically exhibit relatively even flow patterns because they are groundwater driven, as opposed to the flashy flow patterns of streams draining lacustrine plains (Velz and Gannon 1960). Flow regimes can have pronounced effects on stream invertebrate assemblages (Statzner et al. 1988; Robinson et al. 1993). For example, Poff and Allan (1995) found that hydrologic variation plays a large role in structuring fish assemblages in the midwestern United States. Although not measured in this study, stream temperatures of morainal systems may be several degrees cooler than outwash streams. Temperatures have significant effects on invertebrate

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distribution patterns at both local (Haro and Wiley 1992) and landscape scales (Quinn and Hickey 1990*a*). Since central Michigan, as well as much of the upper midwestern United States, is characterized by diverse glacial deposits, their flow regime and temperature influences may be considerable and contribute to the variation observed in macroinvertebrate assemblages at the catchment and basin scale.

Because of confounding factors, the magnitude of influence of land use on stream habitat is difficult to characterize. Low-gradient midwestern streams in the United States are regulated by multiple sets of processes under the influence of subtle topographic gradients, multiple land uses and soil types, variable riparian vegetation, as well as historic and current anthropogenic modifications to streams and catchments. Ditching, channelizing, and hydrologic changes associated with large-scale land cover changes such as agriculture and wetland drainage have a significant effect on current stream physical conditions (Hay and Stall 1974; Verry 1992). Many of these effects were not quantified in our analysis. Nonetheless, some land use influences were apparent. Foremost, the proportion of permanent vegetation in a catchment was vital for mediating other land use impacts on stream habitats. In our preliminary land cover analyses, row-crop agriculture was highly negatively correlated with almost all permanently vegetated land covers. These results indirectly underscore the importance of row-crop agriculture as a determinant of stream condition. We have found (L. Johnson, C. Richards, and G. Host, unpublished data) that row-crop agriculture was also an important predictor of water chemistry variables in these same streams. Agricultural runoff from such areas is frequently associated with increased sedimentation in stream channels (Lenat 1984) and a variety of flow and water quality changes (Menzel et al. 1984). The extent of agricultural development is often strongly associated with compositional changes in macroinvertebrate assemblages among catchments (Corkum 1990; Quinn and Hickey 1990*b*). In contrast, the amount of forested land cover is often related to the quantity and types of detrital and woody debris in streams (Bisson et al. 1987; Richards and Host 1994). These enhance stream habitats and are frequently associated with increased biodiversity of micro- and macro-fauna.

Wetland extent also emerged as an important feature of land use – land cover. Although wetlands represented a relatively small proportion of total catchment area (less than 10%), they influenced several habitat features such as woody debris and some aspects of channel dimensions. Because wetlands mediate surface water flow and hydrology (Mitsch and Gosselink 1986), which in turn influence morphological development of stream channels (Richards 1982), their presence moderates many physical characteristics of streams. In addition, when positioned in stream networks, they attenuate hydraulically driven variables including sediment, nutrients, temperature, and disturbance. Our analyses considered only the total or proportional amounts of wetlands within the catchment; these conclusions do not account for the effect of spatial position. Because other studies have indicated that the spatial position of wetlands within the catchment influences their ability to modify inputs to streams (Johnston et al. 1990), the incorporation of position should further improve the ability of GIS data bases to predict stream habitat quality.

Our results suggest that whole catchments may be as important as 100-m buffers around streams for determining several components of stream habitat. Variables related to hydraulic regime, such as channel dimensions, are influenced more by catchment area and composition than factors specific to stream ecotones (Hynes 1975). Substrate characteristics and bank erosion, on the other hand, were more strongly related to factors influenced by the stream buffer. Riparian buffer strips filter particulate runoff (Osborne and Kovacic 1993) and alter erosion patterns, which in turn influence marginal stream habitats and stream invertebrates (Ormerod et al. 1993; Weatherly et al. 1993). However, the effectiveness of stream buffers is moderated by very local variations in vegetative type and aspect (Rabeni and Smale 1995). Stream buffers less than 50 m can be important for defining elements of stream habitat such as woody debris and shoreline protection (Budd et al. 1987). Stream habitats follow a similar pattern to water quality characteristics. Whereas, some water quality parameters can be modified by local riparian conditions (Osborne and Kovacic 1993), dominant water quality trends of streams among catchments are more strongly related to catchment-wide land use and geology (Omernik 1976; Smart et al. 1981; Close and Davies-Colley 1990).

The minimum resolution of our land-use (61-m minimum mapping unit) and geologic data (>100-m minimum mapping unit) may have impaired our ability to analyze such fine-scale variation in buffer characteristics and further resolve the influence of stream buffers. Riparian vegetative widths less than the minimum mapping unit could not be distinguished from the surrounding land use. In addition, the fate of riparian zones (preservation or development) is often determined by individual landowners on small parcels of land. Landscapes such as the Saginaw Bay drainage are highly fragmented in terms of ownership and under diverse management objectives. These sociological driving factors may not be well predicted by ecological data bases, but may be important determinants of stream quality.

Our observations agree with the growing recognition of the importance of large-scale land use and catchment characteristics as determinants of stream assemblages. Fish distributions at basin scales are strongly related to geologic and climatic gradients (Whittier et al. 1988; Poff and Ward 1989; Poff and Allan 1995) and at smaller scales (among catchments) have stronger associations with land use (Steedman 1988; Taylor et al. 1993). Similarly, macroinvertebrate distributions follow geographic gradients over large scales (Corkum and Ciborowski 1988) but exhibit distinct relationships to land use when comparing catchments within basins (Corkum 1989, 1990, 1992; Quinn and Hinckey 1990*a*, 1990*b*; Tate and Heiny 1995). Although relatively few studies have examined algal assemblage patterns over large scales, these assemblages may follow comparable trends with those of fish and macroinvertebrates (Whittier et al. 1988; Leland 1995). Our study supports these concepts and suggests that the influence of landscape cover characteristics throughout the drainage basin may be as important as riparian vegetation for understanding stream ecosystems.

The ability to partition variance in macroinvertebrate or other stream assemblages based on landscape-scale influences indicates that these communities can be used effectively to develop biological signatures (sensu Yoder and Rankin 1995*b*) of catchment condition. By identifying taxa or community metrics that respond predictably and differentially to land-

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use and geologic patterns, signatures tailored to specific natural or anthropogenic factors can be developed. These signatures can improve the ability of biological indicators or criteria to identify causal factors contributing to stream health. In addition, these approaches can identify landscape features controlling biodiversity patterns in stream systems at reach and landscape scales.

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A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat

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Abstract: We present an evaluation system and framework for determining the relations between processes that generate physical features and how these features are used by fish. This information is essential for long-term management of fish habitat within watersheds. The model is hierarchical at three scales: watershed, reach, and site. Physical characteristics at these scales are separated into attributes, features, or variables that provide information on cause-response relationships. An evaluative framework is proposed along with a logical framework to guide analysis. The framework includes a functional analysis of physical characteristics and processes that generate physical habitat and a functional analysis of habitat requirements related to life cycle of an indicator species. An example of a life stage – state analysis is presented. Concepts of "health," "integrity," and "fit" are used to assess the physical states and conditions of the environment to determine the potential fit for a species based on its life-cycle requirements.

Résumé : Nous présentons un système et un cadre d'évaluation pour déterminer les rapports entre les processus qui sont à l'origine de caractéristiques physiques et pour préciser comment les poissons utilisent ces caractéristiques. Ces données sont essentielles pour la gestion à long terme de l'habitat des poissons dans les bassins hydrographiques. Le modèle comporte trois échelles: bassin, tronçon et site. Les caractéristiques physiques à ces trois échelles sont classées en attributs, en caractéristiques ou en variables qui fournissent des données sur les relations entre les causes et les effets observés. Nous proposons un cadre d'évaluation ainsi qu'un cadre logique pour orienter notre analyse. Le cadre comprend une analyse fonctionnelle des propriétés et processus physiques qui sont à l'origine des habitats physiques et une analyse fonctionnelle des conditions que cet habitat doit présenter en rapport avec le cycle biologique d'une espèce indicatrice. Nous présentons un exemple d'analyse des étapes de ce cycle biologique. Nous utilisons les concepts de « santé », « d' intégrité » et « d'aptitude » pour évaluer l'état physique et les conditions d'un milieu en vue de déterminer dans quelle mesure ce milieu est apte à supporter une espèce en fonction des exigences de son cycle biologique.
[Traduit par la Rédaction]

Introduction

Habitat is being altered throughout the world at an alarming rate. Natural regimes are being altered by modifications to landscapes. Human-induced changes alter aquatic environments often by changing the amounts and distribution of water, sediment, and nutrients released from modified landscapes. These changes in turn create responses in physical, chemical, and biological processes in streams and rivers that are ultimately manifest in the biotic community (e.g., Perrin et al. 1987; Benke et al. 1988; Northcote 1988; Armitage 1994). Most managers and scientists working in flowing water agree that habitat is important for fish and other forms of aquatic life. Structural characteristics of river channels provide the requirements for important and often critical life stages of most stream-dwelling organisms (Bayley and Li 1994). Management of landscapes, habitat, and species will not be successful unless we are able to understand cause-response relationships at various scales within a physically defined ecosystem (Allen and Hoekstra 1992).

Aquatic-systems management and restoration have traditionally focused on site-level strategies (White and Brynildson 1967; DFO and BC 1980; OMNR 1982; Gore 1985; Hunt 1993; White 1996). Recently a number of authors have emphasized that many observed habitat losses at a site may have been due to changes at a reach or watershed scale. These larger scale changes are often left unresolved or are poorly understood (Brookes 1988; Resh et al. 1988; Naiman et al. 1992; National Research Council 1992). Examination of habitat characteristics using a larger context such as watershed, subwatershed, or valley segment units is now being proposed (Warren 1979; Frissell et al. 1986; Naiman et al. 1988; Cupp 1989; Imhof et al. 1991; Naiman 1992). White (1996) provides a synoptic and analytical look at the history of stream restoration works in North America and provides sound suggestions on future directions.

Management of aquatic systems including habitat requires an understanding of relations between the structure and function (process responses) of physical systems; how the animals and plants use these structures as habitat; and where these

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important features are likely to occur within a watershed (Naveh and Liberman 1993). Managers must also understand and be able to predict how proposed changes in land management and land use will affect physical processes operating within watersheds so that these processes and their controlling factors can be protected. Such information will facilitate protection, remediation, or rehabilitation strategies for a system.

To date there has been difficulty linking descriptive habitat features to the processes that formulate change (e.g., erosion-deposition, flows, heating, etc.) and create habitat features measured by biologists and used by animals. Despite the belief in these relationships, biological and physical scientists have difficulty in relating information between their fields. Physical scientists tend to examine aquatic systems in a predictive and analytical way, whereas because of the enormous complexity of interactions of biota and their habitat, biological scientists tend to examine aquatic systems in a descriptive and experimental way (Gordon et al. 1992).

The difficulty faced by ecologists and biologists is trying to understand the range of physical habitat forms, their spatial distribution, and their persistence or rates of change within a stream in relation to how and when animals require these habitat features. There is a strong need for more collaborative work between physical and biological scientists to understand some of these processes (e.g., Gordon et al. 1992). There is also a strong need for further interaction between terrestrial and aquatic biologists and ecologists to understand the linkages and interactions between terrestrial systems and aquatic systems at various scales (valley and stream, upland interactions, floodplain interactions, riparian zone interactions).

An understanding of the processes controlling characteristics of habitat necessary for fish communities is essential to protect these processes and features during periods of land-use change. An understanding of the physical processes operating at certain scales will improve the effectiveness of remediation or rehabilitation efforts. For example, excessive streambank erosion could be a site issue (e.g., overgrazing by cattle), a reach issue (e.g., channel modifications upslope that disrupted the meander pattern), a watershed-level change (e.g., change in hydrology due to agricultural drainage), or a mixture of all of these. Without understanding the linkages of formative processes (causes) to the forms created by these processes (responses), it is difficult to be effective in management or analysis of the problems.

This paper supports the contention made by Petts (1994) for the need to link hydrology, geomorphology, climate, and other physical attributes, features, and variables to the formation of habitat at various scales. We propose a system that characterizes and evaluates information within a logical framework in response to comments on classification and assessment approaches made by Naiman et al. (1992) and Kaufmann et al. (1994). This paper provides the following: (*i*) a hierarchically based framework for characterizing cause-response relations between physical attributes and habitat at three scales: watersheds, reach, and site; (*ii*) an approach to analyzing the interrelationship between the life stages–states of a species and the dynamic and static physical characteristics of their required environments; (*iii*) an evaluative framework for determining the "fit" between a species and the habitat features of the physical environment.

Information derived from the literature for a species, brown trout (*Salmo trutta*) is used to examine interrelationships of life stage to physical habitat and to test the evaluative framework proposed in this paper.

This paper does not examine the relationships between the dynamic processes operating within the field of community ecology, which act as major modifiers to conditions established by physical processes. Nor do we deal with biochemical relationships.

A hierarchical evaluation model

An ecosystem approach to stream management

Numerous authors have recently stressed the need to examine and ultimately attempt to manage human interactions with complex systems from an ecosystem basis no matter how difficult this may be (IJC 1978; Allen and Hoekstra 1992; Allen et al. 1993; Kaufmann et al. 1994). Simple solutions based upon a site remediation perspective have not appeared to work (White 1996). Often the cause of change has occurred over a larger scale than the remedial solutions. For example, there have been many attempts to restore silted-in spawning riffles by the application of gravel to the riffle. These solutions often only work for a few years because the problem is usually the structure of the channel (e.g., width:depth ratio too great for the stream type because of changes in watershed hydrology) or a change in sediment loadings (e.g., excessive soil loss from agricultural fields).

Depending upon the question asked and the information sought, geographically based ecosystem units used for analysis and management may vary (Allen et al. 1993; Kaufmann et al. 1994). A variety of physically defined units can be used given the particular interest (e.g., ecoregion for vegetation; lake basin or watershed for aquatic animals). Inherent is the need to be able to determine a logical geographically bounded unit of space and time in which the inputs and outputs of materials and energy can be defined. Also important is the consideration that trends in movement and processing of material and energy in ecosystems appear to be nested at different scales (Urban et al. 1987; Benke et al. 1988; Minshall 1988; Naiman et al. 1992; Norton and Ulanowicz 1992).

Many descriptive models for fish and fish habitat do exist and can estimate biomass based upon certain habitat variables. They often fail when employed in different geological or climatic areas or when used to predict impacts on fish biomass based upon changes in habitat variables (see review by Bowlby and Roff 1986*a*; Fausch et al. 1988).

At present we are unable to predict impacts of watershed change on fish because we are unable to predict impacts of watershed change on habitat and in some instances linkages between fish and habitat (Fausch et al. 1988). The link between formative processes and habitat is missing. Information on these linkages between cause and response are critical if biologists are to work with physical scientists to manage, conserve, or restore watersheds or portions of watersheds. Equally important is the need to understand that various physical formative processes are occurring at different scales. Given that species and processes interact over a wide range of scales (Harris 1980, 1986, 1994; Allen and Hoekstra 1992; Benda et al. 1992), it is imperative that any framework incorporate a consideration of scale in time and space.

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There is a need to synthesize information and develop general relationships of ecosystem functioning to place specific cases in appropriate spatial, temporal, and analytical context (Allen and Hoekstra 1992; Naiman et al. 1992). Most comparisons between ecosystems have tended to be horizontal (i.e., side by side) versus vertical (i.e., upscale-downscale) and descriptive rather than predictive (Allen and Hoekstra 1992; Harris 1994). Harris (1994) urges the creation of a conceptual basis and the development of quantitative ecological relationships from which some level of predictive power is achieved.

In this evaluation model, we propose that information be structured in a way that differentiates cause-response relationships between physical and biological attributes, features, and variables of an ecosystem. This information would aid in the examination of the three descriptive elements of ecosystems: composition (the individual biotic and abiotic elements of the system), structure (the form these elements take on the landscape), and function (how the elements and form interact) (e.g., Swanson et al. 1982; Noss 1990; Kaufmann et al. 1994). Most studies of habitat-fish interactions define structural habitat in relation to how fish utilize it rather than how that structural habitat forms and changes. New information is being developed to address the dynamic nature of habitat (Nelson et al. 1992; Benda et al. 1992). Without this understanding it is difficult for managers to determine how changes in physical processes at various scales will be manifested in habitat change (Armitage 1994; National Research Council 1994).

Hierarchy and scale

Schumm and Lichy (1965) suggest that, at small scales, physical forces acting on a site appeared to be disruptive; however, if viewed at a larger scale the forces exhibit a trend towards some equilibrium state (see Leopold et al. 1964; Bormann and Likens 1979; Allen and Hoekstra 1992).

Scale and hierarchies of scale within ecosystem units are discussed by a number of authors (e.g., Naveh and Liberman 1983; Frissell et al. 1986; O'Neill et al. 1986; O'Neill 1989; Noss 1990). O'Neill (1989) states that, to understand various processes and their effects, it is important to examine them within the appropriate temporal and spatial scale. Hierarchical systems tend to be nested (Allen and Starr 1982; O'Neill et al. 1986; Allen and Hoekstra 1992). This refers to the control that larger scale variables have on finer scale variables. Therefore, it is important to define the cause-response linkages between different scales.

This is not a simple matter given the complexity of ecosystems. In this model we selected processes that operate across scales and, thus, define critical linkages (e.g., runoff generation, sediment load and transport, erosion-deposition, and vegetative interaction or succession). These processes are assessed in terms of the physical variables, features, and attributes that are manifested at the scales of watershed, reach, and site (Allen and Hoekstra 1992; Harris 1994). The proposed model uses certain processes to describe cause and response within and between scales (as suggested by Allen and Hoekstra 1992; Harris 1994; Fitzgibbon and Imhof 1994). This conceptualization is familiar to those involved in modelling watershed flow and sediment regimes. However, it requires going a few steps further and modelling the responses of streamflow and channel form to runoff and sediment load changes in the system at different scales and linking these to models of habitat systems at the appropriate spatial scale. For example, changes in the sediment regime at a watershed scale are manifested by soil loss and gullying. At a reach scale the same phenomenon can be seen by changes in channel gradient, substrate, and channel form. At the site scale, sediment regime changes can be seen in adjustments to cross-sectional shape of the channel, patterns of erosion and deposition, flow characteristics (i.e., depth and velocity), and habitat (i.e., shelter or living space).

The effectiveness of interactions within the hierarchy of scales in a watershed depends upon how the processes operate and are linked. Therefore, some processes and elicited responses at a larger scale may not link together to modify processes at a finer scale (Baker 1989; Bendix 1994).

Stream habitat in space and time

Hierarchical approaches have been widely used recently to classify and assess habitat characteristics of watersheds, valleys, and rivers (Warren 1979; Frissell et al. 1986; Naiman et al. 1988; Cupp 1989; Rosgen 1994). The objective of these approaches is to develop methods to characterize physical systems and in some instances to develop typologies (Harris 1988; Cupp 1989; Rosgen 1994). For example, both Cupp (1989) and Rosgen (1994) use controlling or state conditions (e.g., valley slope, entrenchment) to define classes or types of valley forms (Cupp 1989) and stream channel forms (Rosgen 1994) that characterize the form and function of these systems. Both these approaches use hierarchically based variables to classify or type their system of interest.

Naiman et al. (1992) review the general principles related to classification and assessment of rivers. They suggest that several characteristics are very important components of any classification system developed for rivers and watersheds: (*i*) longitudinal and lateral linkages; (*ii*) changes occurring in physical features over time; (*iii*) boundaries between apparent patches that are often indistinct; and (*iv*) geomorphic and ecological characteristics that vary spatially from headwaters to mouth and temporally in response to disturbance patterns.

Naiman et al. (1992) and others (Gregory et al. 1991; Kaufmann et al. 1994; Fitzgibbon and Imhof 1994) also suggest that the development and relationships of these measurements pose a problem for classification systems of rivers and watersheds. However, these requirements for habitat linkages and habitat variability are also identified as essential for the long-term maintenance, vitality, and resiliency of streams and watershed ecosystems (Naiman et al. 1988, 1992; Kay 1991*a*, 1991*b*; Kaufmann et al. 1994).

Frissell et al. (1986) propose a hierarchical framework that extends from watershed to stream system, segment system, reach system, pool-riffle system, and microhabitat system (Table 1). Vertical and lateral dimensions are discussed, but linkages and interactive pathways are poorly defined especially between the channel and its floodplain and riparian zones (see Naiman et al. 1988). This inadvertent omission must be addressed (Imhof et al. 1991; National Research Council 1992; Naiman et al. 1992; Petts 1994).

Table 1 is modified from a previous table of Fitzgibbon and Imhof (1994) that used as its foundation information in Frissell et al. (1986). As a basis for practical analysis we consider watershed systems ranging from the tertiary level or third order (in watershed ranking) to the habitat element level: water-

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Table 1. A proposed hierarchy for the determination of the scale of measurement for geographic, geomorphic, and biotic data collection and analysis within watershed systems (some elements modified or adapted from Frissell et al. 1986).

System level	Linear spatial scale (m)	Areal spatial scale (m^2)	Areal and profile boundaries	Time scale of continuous potential persistence (years)	Time scale of persistence under human disturbance patterns (years)	Biotic assemblage scale	Life activity and scale (variable time)
Watershed	10^5	10^{10}	Drainage divides between tertiary watersheds	10^6–10^5	10^4–10^3	Community species (migratory)	Life cycle (<20 yr)
Subwatershed	10^4	10^8	Drainage boundaries of quaternary watersheds within tertiary drainage basins	10^4–10^3	10^2–10^1	Community/ species	Life cycle (1–8 yr)
Reach	10^4–10^1	10^5	Minimum of two full channel wavelengths, and defined by as a specific stream type based on the Rosgen (1994) classification; active profile boundaries up to 1:20yr flow elevation, passive boundaries to 1:100yr flow elevation	10^2–10^1	10^1–10^0	Species	Life cycle/ life stage (0.1–8 yr)
Site	10^1–10^0	10^2	Channel segment comprising either a riffle or pool, profile including bankside riparian vegetation up to bankfull elevation	10^0	10^0–10^{-1}	Individual	Life stage (0.1–0.4 yr)
Habitat element	10^0–10^{-1}	10^1	Zones of variable substrate types or characteristics, water velocity and depth within either a pool, step or riffle	10^0–10^{-1}	10^{-1}–10^{-2}	Individual	Activity (10^{-3}–0.1 yr)

shed, subwatershed, reach, site, and habitat element. For example, within the Great Lakes basin, tertiary watersheds in regions such as southern Ontario have a linear scale of 10^5 m and an areal scale of approximately 10^{10} m^2. Subwatersheds are sub-drainages of tertiary watersheds. A reach is defined as a portion of valley and stream with a stream length of a minimum of two full wavelengths of a specific stream type (e.g., Leopold et al. 1964; Rosgen 1994). The reach includes the riparian zone and floodplain of the adjacent valley. The lateral extent of a reach changes with a change of stream or valley type. The active-profile boundaries of a reach are up to the 1:20 yr flow elevation, and the passive boundaries to the 1:100 yr flow elevation (after Hill et al. 1991). The 1:100 yr elevations in Ontario are often the edges of the valley walls as discussed by Cupp (1989) (in his valley classification). A site is defined as either a riffle or pool component of a reach. The active profile boundaries of a site include bankfull elevation and bankside riparian zones and point bars. A habitat element is defined as an area relatively homogeneous within the riffle or pool segment.

The range of linear scale of the reach, site, and habitat element scales reflects the variability based upon size of streams of different order. Like Frissell et al. (1986), we identify both linear scale and temporal-persistence scales. We also believe there is a strong need to identify and quantify the areal extent of scale to address the importance of the channel and its floodplain and riparian zone as well as the relative persistence of features under land-use modification.

The hierarchical matrices presented in Tables 2, 3, and 4 are modifications of matrices presented by Fitzgibbon and Imhof (1994). These matrices are used to characterize a watershed system at three major scales of management: watershed, reach, and site. Biologists most often operate on a practical basis at the site level, geomorphologists at the reach level and hydrologists at the watershed level. This model sequence is developed to provide practical means of characterizing a system at these three management levels. These three scales are similar in space and time to the hierarchical scaling for riparian systems discussed by Gregory et al. (1991) and for fish habitat by Frissell et al. (1986). Godfrey (1977) and subsequently Frissell et al. (1986) suggested that a number of benefits arise from use of hierarchical characterization: (*i*) classification at higher levels narrows the set of variables needed at the lower levels; (*ii*) it provides for integration of data from diverse sources and of different levels of resolution; and (*iii*) it allows the scientist or manager to select the level of resolution most appropriate to his or her objectives.

The matrices presented in Tables 2, 3, and 4 support one key contention of hierarchical analysis: that process rates should be grouped into distinct levels. This approach is in keeping with observations of O'Neill (1989) who states, "Hierarchical considerations predict that a complex system will not show rates uniformly distributed between the fastest and slowest rates. Rather, the rate processes will be grouped into distinct levels." For example, changes in watershed slopes that adjust valley slopes occur over long geological periods, often controlled by climate (e.g., glaciation) or geology (e.g., plate uplift). The slope of a reach is controlled by the valley slope and is adjusted cumulatively over a period of years by changes in sediment and flow regimes (Leopold et al. 1964). The reach responds by adjusting sinuosity and, therefore, effective slope. At the site level, the change in slope depends on the shifting

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Table 2. Watershed characterization (linear scale 10^5; areal scale 10^{10}) matrix providing an information structure to differentiate causal attributes from effects on form and the habitat attributes provided by the form.

Causes		Effects		
State	Condition	Process(es)	Response	Habitat
Climate	Precipitation and snowmelt regimes	Runoff, infiltration, evapotranspiration	Drainage density (recharge:discharge and surface and subsurface runoff)	Stability and diversity of habitats is expressed by the regime characteristics of the formative (bankfull) and stress (lowflow) flows
	Temperature	Heating	Stream temperature regime	Thermal stress and ranges (e.g., cold or warmwater communities)
Landform (geology: physiography) modifier, watershed slope	Slope stability	Slope and channel erosion	Sediment load; entrenchment; valley slope	Floodplain width and diversity of features (e.g., terraces, cutoffs, swales, oxbows) Potential stream types Controls diversity of channel characteristics and therefore habitat potential
Landform (geology: physiography) modifier, sediment type	Sediment stability and source	Sediment transport;	Sediment load, type and size;	Ratio of suspended sediment vs. bedload volumes (mass per unit mass)provides measure of habitat stability; substrate types measure of potential uses
	Porosity, depression storage	Infiltration; discharge (runoff; high and low regime and yields)	Drainage density; downstream channel geometry	Flow regime; flow contributing areas; living space
	Relative alkalinity	Redox and oxidation	pH	Productivity
Landcover	Infiltrability	Runoff:recharge	Flow regime	Temporal volume of living space
	Erosivity	Sediment, nutrient and carbon transport	Sediment load and bank slope	Floodplain and riparian vegetation
			Productivity	Biomass, diversity and growth rates

of riffles and pools during relatively short-term events that occur within a period of one to several years (Leopold et al. 1964; Leopold 1994).

Frissell et al. (1986) also discuss examples of hierarchical scales and controlling forces operating on small-scale systems (e.g., riffle-pool morphology set by slope of reach and inputs of sediment and water from drainage basin above) and the contextual framework necessary to understand them (see also Schumm and Lichy 1965). With the exception of Frissell et al. (1986), the difficulty with some approaches is that they are either complex and labour intensive or are focused only on one or two scales such as basin scale, valley, or reach without due connection to the other scales (see review in Naiman et al. 1992).

Physical habitat indicators

Indicators[2] were selected from a variety of sources (Leopold et al. 1964; Morisawa 1968; Schumm 1972; Rosgen 1994). Habitat features and variables for the various indicators are drawn from a number of sources (Hynes 1970; Lotspeich 1980; Lisle 1981; Lotspeich and Platts 1982; Décamp 1984; Bowlby and Roff 1986*a*; Fausch et al. 1988; Harris 1988; Naiman et al. 1988; Statzner et al. 1988; Wright et al. 1989; Gregory et al. 1991; Matthews et al. 1991; ASCE 1992; Gregory 1992; Lisle and Lewis 1992; Nelson et al. 1992). The number of indicators in these tables are relatively few and will hopefully allow for a reasonable and practical means of quantifying and understanding cause-response relationships at and between the various scales. We would suggest that these indicators provide the minimum information necessary to link physical processes to habitat attributes and a practical means of qualifying cause-response relationships at and between scales.

Information that is relevant for each scale is placed into a specific category (see Tables 2, 3, and 4). These categories are state, condition, process(es), response, and habitat. These categories are defined as follows:(*i*) state, the normative characteristic (i.e., static) of the system for the specific scale being examined (i.e., climate; e.g., humid, north temperate[3]); (*ii*) condition, the variations of the particular normative characteristic (i.e., weather; e.g., precipitation regimes); (*iii*) process(es), the operations of the particular system (e.g., runoff generation); (*iv*) response, the physical response or forms of the system to the processes (e.g., drainage density); and

[2] Indicators may be variables, features, or attributes.

[3] Watershed-scale examples are given for each category.

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Table 3. Reach characterization matrix (linear scale 10^3–10^1; areal scale 10^5) providing an information structure to differentiate causal attributes from effects on form and the habitat attributes provided by the form.

Causes		Effects		
State	Condition	Process(es)	Response	Habitat
Runoff Flows				
Baseflow groundwater magnitude and duration (e.g., $_7Q_5$, $_7Q_{10}$, $_7Q_{20}$)	Velocity; livings pace	Respiration	Metabolic stress	Depth, area, oxygen level, temperature
Bankfull – channel forming (1:0.7 – 1:1.7 yr)	Velocity, depth	Erosion, deposition	Channel geometry (i.e., width/depth, sinuosity, etc.)	Aquatic structural habitat (see Table 5)
Riparian flows (1:2 – 1:20 yr; organic matter exchange)	Velocity, flooding	Erosion, deposition and inundation (durational and depth)	Floodplain formation; nutrient exchanges; debris movement; migratory access	Riparian/terrestrial habitat, reproductive space
Floodplain –system reset (1:20 – 1:100 yr)	Velocity, flooding	Erosion, deposition	Channel slope, floodplain forms	Valley terrestrial habitat
Slope				
Riffle slope	Energy gradient	Erosion, deposition (lateral)	Channel sinuosity	Relative divers ity of living space (riffle–pool or step–pool types); spacing
Pool slope	Friction gradient	Erosion, deposition (lateral)	Width:depth ratio	Structural complexity; vertical channel variability
Sediment				
Sediment size range	Roughness	Erosion, deposition	Width:depth, channel shape	Habitat structure diversity
Sediment load	Channel stability	Erosion, deposition	Width:depth, sediment size, sorting	Habitat structure stability
Vegetation				
Community	Roughness, bank cohesion	Succession; erosion, deposition	Woody debris; width:depth, bank stability	Shelter, nutrients
Age	Roughness, shading	Flooding, erosion, deposition, heat transfer	Width:depth; channel complexity	Temperature, refuge
Density	Roughness, cohesion	Flow velocity, erosion/deposition	Bank slope; bank stability	Habitat refuge stability

Table 4. Site/cross-section characterization matrix (linear scale 10^1–10^0; areal scale 10^2) providing an information structure to differentiate causal attributes from effects on form and the habitat attributes provided by the form.

Cause		Effects		
State	Condition	Process(es)	Response	Habitat
Flow velocity and depth (bankfull)	Shear stress (in the flow)	Erosion; deposition	Bed/bank form (planform)	Relative amounts of spawning, resting, refuge, and ambush areas of a stream type for a given species
Width:depth	Friction	Erosion; deposition	Channel shape (cross-sectional)	Determines volume of living space and relative utility for various life stages
Slope (water surface)	Shear stress (on the bed)	Erosion, deposition	Channel forms, substrate characteristics (i.e., riffle:pool or bar)	Differentiates life cycle requirements and activities (e.g., high slope, feeding/reproduction; low slope, refuge/ambush)
Cohesion (bank)	Shear strength	Erosion	Bank slope	Refuge areas, ambush (e.g. undercut banks)
Sediment size (sorting D_5,D_{15},D_{85})	Roughness, shear strength	Erosion, transport	Riffles, pools, bars	Benthic habitat, spawning areas, shelter
Boulders	Friction	Erosion, deposition	Channel shape	Refuge
Large woody debris	Friction	Erosion, velocity	Width/depth, bank slope, deposition, nutrients	Refuge, spawning areas; food for invertebrates (productivity)
Riparian vegetation (succession)	Friction, cohesion	Erosion, deposition	Bank slope, shading	Refuge areas, temperature moderation, and nutrients as a food source

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Table 5. Life stage/state characterization for brown trout (*Salmo trutta*) in relation to dynamic processes, physical characteristics and required habitat attributes and their interactions (see Fig. 1).

Life stage or state	Dynamic conditions	Physical environment (static condition)	Habitat
Reproduction	Erosional zones	Outwash gravels and sands	Typical in riffle – pool systems; less in step – pool systems
	Fall spawners – October to November	Gravel moraines	Spawning occurs at head of riffles, often along margins with adjacent cover of logs and overhangs
	$v > 30$ cm.s^{-1}, $d > 30$ cm	Sand and gravel tills	>400mm depth of substrate necessary for spawning; low % fines in pavement
	Interflow of water through the redd with near saturated O_2 levels through period of incubation	May be limited in bedrock controlled systems	
		Less in till/clay plains	
	Groundwater moderated winter flows	$D_{50} = 20$ mm (coarse gravel substrate)	
		Less spawning in flat dominated riffle:pool systems, evident of active bedrock control	
Nursery	Depositional zones	Sands and silts	Shelter and feeding (passive)[a]
	Very low velocities	Shallow depths with high roughness, often with vegetation and (or) woody debris and detritus	Riffle margins in the lower half to third of riffles, especially at the tail of riffles
			Linked to spawning areas
Juvenile	Erosional zones	Cobble and boulder	Feeding and shelter (active)[b]
	Fast water, shallow to moderate depth	Rough bottom with structural diversity that allows good distribution of territory	Mid to head of riffles also at the tail out to the pool
Overwinter habitat	Depositional zones	Structural complexity	Refuge and shelter, feeding (passive)
Juvenile and adult (see also flow requirements)	Continuous low velocities	Variable in space	Pools and (or) cut banks adjacent to pool area
	Depth	Best in physiographic units that allow deep pool formation and active groundwater systems	Usually bottom third of pools
	Groundwater flow regime (seepage)		Undercuts at cut banks, also associated with logjams with one or both cut bank and (or) pool
Adult /shelter	Depositional zones (although variable)	Medium to high structural complexity	Spatially variable:
	Stable depths	Woody debris for shelter	Active and passive feeding; shelter
	Significant velocity gradients	Variable in space	Predominantly in pools of first- to fourth-order streams
		Best in physiographic units that allow deep pool formation	Inhabit riffles with good structure in third- to sixth-order streams
			High roughness of bed and banks ideal
			Woody debris is an enhancement factor
Feeding (active)	Erosional zones	Feeding areas need to be close to shelter	Feeding is dominant in transitional zones, head of riffles during invertebrate drift or emergence and tail of pools during ovipositing
Environments	Feeding areas should support diverse prey assemblage with good biomass	Coarse bottom substrates in high gradient areas comprised of gravels, cobbles and boulders	
Food habitats	Macroinvertebrates major food item during early stages of life		
	Depositional zones for minnow species (important food item in older mature fish)	Substrate variable, depth and volume more important for minnow species	Pool and shallow slow or fast areas used as foraging areas for minnow species
Migration	Flow regimes: high and low	Drainage density an indicator of groundwater vs. surface-water fed systems	Ideal reproductive/nursery areas in first- and second-order streams with good low flows although may range up to third- to fourth-order streams
Reproduction	High flows: opportunity for movement to reproductive zones and movement of juveniles out of system		
Seasonal habitat use	Low flows: control density and survival on an event and regime basis depends on size and location of stream	Fine soils generate large drainage density – low baseflows compared to low drainage density and large baseflows	Juveniles and adults in second- to fourth-order streams
			Overwintering areas often confined to third- to fifth-order

[a]Active, animal actively seeks and pursues food.
[b]Passive, opportunistic feeding only.

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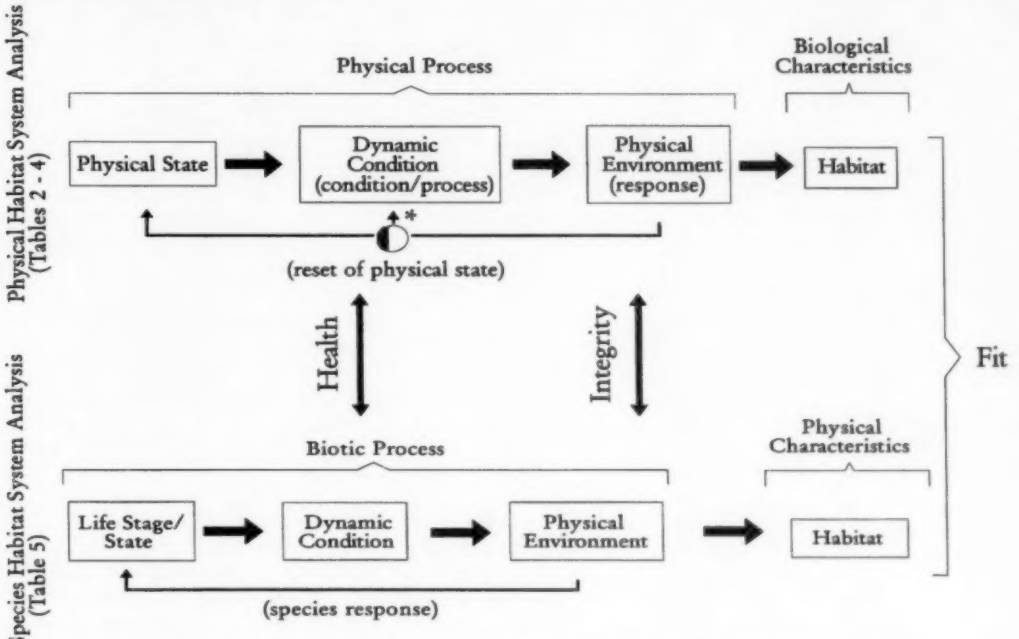
Fig. 1. Flowchart models demonstrating the major elements of the physical habitat and species habitat analyses presented in the two series of tabular matrices discussed in the paper.



*Splitter, dividing an input into 2 or more parts (see Talbot & Gessner 1973).

(*v*) habitat, the habitat measure for the effect created by the process controlled by the state (e.g., potential habitat volume in the channel).

The proposed system of indicators defined in this paper provide a hierarchical characterization and information structure that links the different scales from watershed to the site (Tables 2, 3, and 4). These matrices are designed to: (*i*) structure information; (*ii*) separate out indicators that identify state and condition from processes and responses; (*iii*) link the habitat indicators derived from the interaction of cause and response to a particular state indicator; and (*v*) provide a basis for the examination of the types of habitats in relation to a particular species of interest in the system (see discussion of Table 5).

The hierarchical model and framework presented in this paper uses and modifies an approach espoused by Kaufmann et al. (1994) and others (Hunter 1990; Turner and Gardner 1991; Jensen and Bourgeron 1993). Their approach calls for the characterization of a system, determination of important attributes, and identification of cause-effect relationships based upon work done by Hunter (1990). Hunter's procedure uses a two-step approach referred to as "coarse-filter analysis" (physical or large-scale analysis) and "fine-filter analysis" (biological or fine-scale analysis). We build upon this approach using physical habitat and species habitat analyses applied a three defined scales. Figure 1 presents the two analytical systems: the physical habitat system and species habitat system. These system diagrams draw upon concepts described by Bennett and Chorley (1978). Figure 1 identifies the relationships between the major components of the two systems to provide a framework for analysis of the indicators in Tables 2, 3, 4, and 5. Reset mechanisms (i.e., adjustment or recovery to a stable state or condition) occur in both the physical system and species system (Fig. 1). A "splitter" symbol (see Talbot and Gessner 1973) is used to indicate that some resets can alter processes, and at times, state. Resets in physical processes occur as a result of disturbance. These disturbances can occur at various spatial and temporal scales and can have different impacts of the system (see Resh et al. 1988; Kay 1991*a*, 1991*b*). The reset function also acts as a feedback downscale so that physical forms and processes generated at one scale become the state variables at the next scale below (i.e., nested or hierarchical interactions). This generates a "cascade" of cause-response relationships suggested by O'Neill (1989) and O'Neill et al. (1986). Changes in the physical conditions due to disturbances modify physical process responses, which in turn alter physical habitat (Resh et al. 1988; Kay 1991*a*; Kaufmann et al. 1994). In turn, species must respond to these new habitat states and conditions or be displaced.

The model outlined in Tables 2, 3, and 4 provides a framework for functional assessment of a watershed at three scales. It helps to determine whether the physical system that occurs within the watershed is to be expected given the geology, climate, soils, and valley characteristics. Analysis of information from the watershed can be used to determine the specific characteristics of the system and to determine the potential impacts of changes in both the state of the watershed and conditions affecting it. These tables can also be used to: (*i*) determine appropriate information that needs to be collected at the selected scale of analysis; (*ii*) determine the appropriate

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scale in which to collect information on a specific feature of interest; and (*iii*) strategically determine the appropriate scale for planning and intervention processes.

Response of biota to spatial and temporal habitat dynamics

Biota living in flowing water are adapted to the dynamics typical of this type of environment (e.g., Hynes 1970; Minshall 1988; Bayley and Li 1994; Power et al. 1995). Life-history stages of these lotic biota must be adapted to changes that occur at different spatial and temporal scales. For example, examination of invertebrate communities by Statzner and Higler (1986) and Statzner et al. (1988) and the work by Fausch et al. (1988), who examined habitat variables important in the prediction of fish biomass, suggest strong relationships between physical habitat dynamics and biotic use.

Two major analytical components are necessary to determine how well an particular species is suited to a stream within a particular watershed: knowledge of the life-history requirements in space and time and knowledge of the availability of physical habitat features in space and time. Physical habitat analysis of the system can assess the potential availability of habitat throughout the watershed over time. An examination of the needs of the species in relation to available habitat is required to determine how well the physical system is suited for a particular species (e.g., Bayley and Li 1994). For example, migratory fish such as salmonids move extensively throughout a watershed during their spawning runs. Therefore, habitat for reproduction within a watershed is contingent upon a flow regime that supports migration to potential spawning areas. Successful spawning migrations are achieved through flows of appropriate timing, magnitude, and duration (Trush 1989).

If we accept that habitats are generated by physical and chemical processes of the environment, then examining the habitat requirements of a species' life stages should provide an effective means of identifying critical and sensitive physical habitat requirements in terms of space and time. This type of analysis should allow characterization both in physical and biological terms and provide a tool for the identification of the "fit" of a species with its environment at the appropriate scales in space and time. We suggest that an animal would "fit" with its environment if there was a spatial and temporal coincidence between the species' life-cycle requirements and the spatial and temporal characteristics of the specific system.

Table 5 is an example of an analytical framework using life-stage analysis of the habitat requirements of a species. Table 5 includes the following categories:

(1) Life stage or state is the normative activity (e.g., reproduction) of a species. This includes a specific stage of a species' life cycle plus activities common through the entire life cycle (e.g., feeding).

(2) Dynamic conditions are those conditions that change rapidly to affect life stage or state activities.

(3) Physical environments are those conditions that must exist over long periods of time to support habitat (e.g., hydrologic, geomorphic, hydraulic).

(4) Habitats are those spaces that have appropriate forms and conditions to support life stages or states.

General and standard life-history stages are used, similar to those used in habitat suitability models (e.g., Raleigh et al. 1984): reproduction, nursery, juvenile, and adult. As well, life-state variables are also used: overwinter refuge, feeding, and migration. This information is used as part of the species habitat systems analysis described in Fig. 1.

The flow charts in Fig. 1 illustrate how Table 5 is used in conjunction with Tables 2, 3, and 4. Analysis of the information in Table 5 in relation to information in the other tables can be used to identify potential habitat availability. Where particular habitat features are limited in time and space they are termed critical habitats. Where these particular features are missing, they represent a lack of fit of the species with its physical environment.

Application of the framework

Figure 1 should be used in conjunction with a logical framework that provides a stepwise structure for analysis. Figure 2 presents the types of logical questions relevant to determining characteristics, habitat features developed, and how well these features fit with the needs of the target species. The questions provide the linkages within and between the physical habitat system and species habitat system analyses (Fig. 1). Question 6 is of special importance to fish habitat managers. This is the step that takes us towards a determination of appropriate actions and interventions for a target species within a watershed. In the following sections we clarify several terms.

Health

Health has two components. Health of the physical environment is defined by the correspondance between the physical state, dynamic conditions and responses (e.g., Schaeffer et al. 1988). Health of the environment for a species is defined by the correspondence of the dynamic conditions provided by the physical environment in relation to those required by the species (e.g., Rapport 1989).

Integrity

Health and integrity are interrelated; however, for the purposes of this paper, integrity for a species exists when the structure (form) and functions of the physical environment match those required for the life stage or state requirements of the species (Torrible 1994).

Fit

A species fits with its physical environment when there is a spatial and temporal coincidence between the species' life stage or state requirements and the spatial and temporal characteristics of the physical environment. Fit provides the integration between health and integrity.

Habitat

Habitat refers to the presence and availability of living space for a species within the system.

An example of model application

To illustrate the application of the logic and analysis frame-

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work, consider the steps necessary to determine the suitability of brown trout for a particular watershed. We have developed a species habitat system matrix for brown trout, a top-level predator residing in cold-water riverine systems (Table 5). Information on the fish and its habitat requirements at various states or stages of its life cycle comes from various literature sources (Shirvell and Dungey 1983; Raleigh et al. 1984; Cunjak and Power 1986; Wesche et al. 1987; Heggenes et al. 1993). Some argue that examination of the requirements of top-level predators provides insight into the health of the system for other lower trophic level organisms (Bowlby and Roff 1986*b*; Northcote 1988; Perrin et al. 1987; Power 1990, 1992; Power et al. 1995). For a food chain to be functional, the ecosystem must provide appropriate habitat for all trophic levels. Thus, the use of a top-level predator as an indicator species for the ecosystem is useful (e.g., Bowlby and Roff 1986*b*).

The hypothetical watershed has a physiography that is indicative of high recharge and discharge capabilities (e.g., gravel moraines, outwash gravel, and sands) typical of those found in some areas of the Great Lakes basin (e.g., Chapman and Putnam 1966). We would expect state conditions to include high porosity, depression storage, and deep percolation. The watershed lies within a humid north temperate climatic zone. This would generate relatively stable, season to season flow rates. Various measures of estimating flow stability are available (e.g., Tennant 1976). These measures are used to examine habitat quality and as a measure of the relationship between climate and physiography. The watershed also has a high percentage of forested land cover (e.g., >20%). This characteristic would reduce erosion and in conjunction with the physiography enhance infiltration and groundwater storage and discharge.

Given the state of the watershed, are the responses (e.g., sediment and flow regimes) and the physical habitats (e.g., riffles and pools) what would be expected (Fig. 1) given our understanding of the processes and experiences with similar type watersheds (question 2)? Let us assume that the regimes are as expected except for portions of poorly managed agriculture in the headwaters. Therefore, dynamic conditions would be slightly altered from what would be expected (i.e., changes in sediment regime resulting from flushes of fines off exposed fields). This would result in changes in sediment load characteristics and substrate composition.

Question 3 asks whether all the physical parts are available for the species. Let us focus on reproduction. Table 5 indicates that brown trout spawn at the head of riffles. Eggs require an active interflow of water through a coarse substrate (Everest et al. 1987; Chapman 1988). Substrates composed primarily of gravels with some sands and low silts allow active movement of water through the spawning redds. Substrates are most actively sorted at the head of riffles at the transition points from pool to riffle. These conditions occur most frequently in meandering gravel-bed riffle-pool streams classified as "C4" type channels (Rosgen 1994) or occasionally in lower slope step-pool streams such as "B4" type streams (Rosgen 1994). These streams occur in watersheds containing gravel moraines or in valleys comprised of outwash gravel and sands. Therefore, integrity of the system assumes that the required physical parts of the system that the species requires for reproduction are present in the system (i.e., gravel moraines or outwash gravels and sands, riffle-pool stream, and well-sorted gravel substrate). However, given the agricultural activity in this hypothetical watershed, the water circulation in gravel riffles has been reduced by excessive fine sediments. This would be observable at the reach and site scale (e.g., Everest et al. 1987; Chapman 1988).

Question 4 asks does the species fit with the environment? Given the increases in fines in the gravel riffles, health of the watershed for brown trout is impaired, resulting in reduced reproductive success (Everest et al. 1987; Chapman 1988; Platts et al. 1989; Lisle and Lewis 1992). Integrity remains intact but is threatened by the loss of quality in the spawning areas. Therefore, the species fits with the environment but the physical environment within the watershed only partially fits with the species because of agricultural activities.

Based upon the above analysis, the habitat of the watershed is disturbed, but sufficient functions remain to provide presence of a population at some level of maintenance (question 5) as long as the other life stages or states fit with the physical environment. With the elevated sediment discharges from agriculture, a Remedial Action Plan (question 6) must be undertaken to improve the health of the system and enhance the fit of the species with the environment within this watershed.

Management considerations

Human disturbances at a watershed scale appear to be relatively rapid in comparison with natural disturbances (Table 1). Anthropogenic disturbances can include land development for urban and agricultural uses, forestry, and mining. These land-use changes alter the runoff regime and sediment production from the watershed. In turn, these changes result in valley and stream channel changes at the subwatershed and reach, thereby altering flows and patterns of erosion and deposition causing changes in hydraulic geometry and substrate material. The relationship of the channel and its floodplain also changes through alteration of overbank flows, erosion and deposition, and interactions with the floodplain resulting from changes in meander dynamics (e.g., Gregory 1992). Changes in channel reach characteristics alter the cross-sectional shape of the channel, the distribution of riffles and pools, point bar forms and composition, thalweg depth and planform, and the slope of the channel. At the site level these changes alter aquatic habitat quality by reducing pool area, depth, and complexity; modifying the sorting and size distribution of particles in the substrate required for invertebrate production (e.g., Statzner et al. 1988) and fish reproduction (e.g., Platts et al. 1989; Lisle and Lewis 1992); changing the distribution of roughness elements in the channel (e.g., Lisle 1981); and disconnecting the channel from floodplain areas (e.g., Junk et al. 1989; Bayley 1995).

Capacity to manage states and conditions at certain scales is limited. For example, at the watershed scale we tend to characterize the system based upon state indicators such as geology, physiography, climate, and land cover. With the exception of land cover and land use, it is difficult to modify, adjust, or manage these states. However, the above state indicators do influence the reach and site states, which can be modified by human activity.

The best management strategy is to maintain functional channel, valley, and watershed characteristics and actively manage human activities that negatively affect natural sys-

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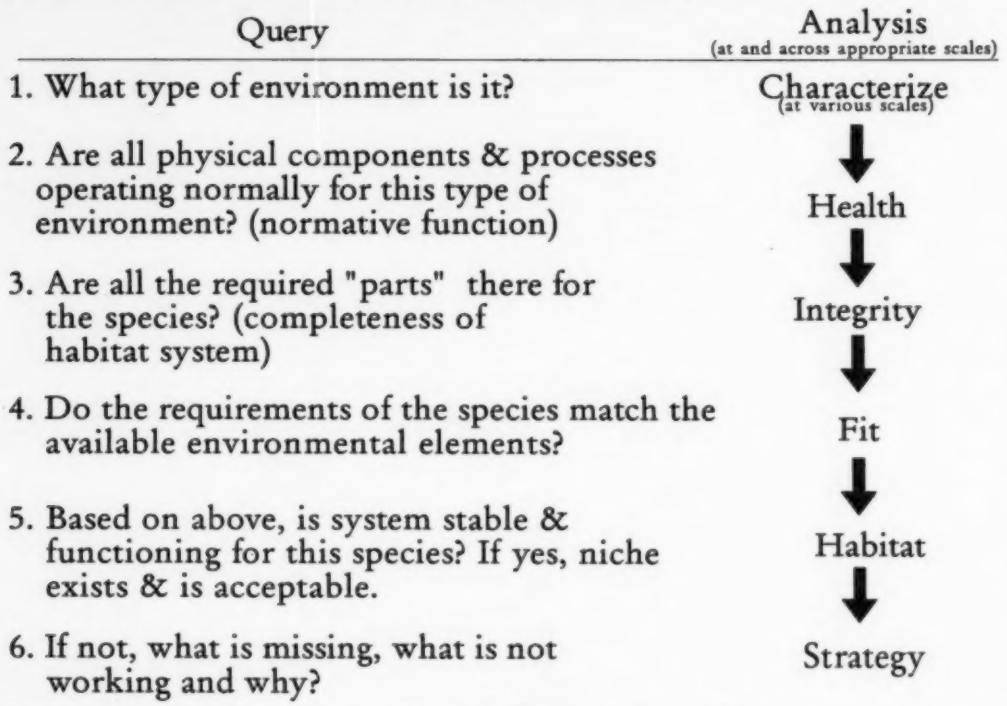
Fig 2. Logical framework of questions used to carry out the system analyses identified in Fig. 1 and Tables 2, 3, 4, and 5.


Query
Analysis
(at and across appropriate scales)
1. What type of environment is it?
Characterize
(at various scales)
2. Are all physical components & processes operating normally for this type of environment? (normative function)
Health
3. Are all the required "parts" there for the species? (completeness of habitat system)
Integrity
4. Do the requirements of the species match the available environmental elements?
Fit
5. Based on above, is system stable & functioning for this species? If yes, niche exists & is acceptable.
Habitat
6. If not, what is missing, what is not working and why?
Strategy

tems. Where systems are severely altered or destroyed, the strategy then must be to restore. McPhee (1989) and Cummins (1992) suggest that the most arrogant of human notions is the idea that we can "actively" and constantly manipulate natural systems rather than maintaining them in a healthy state.

The hierarchical evaluation framework presented in this paper should provide managers with information on the characteristics of a system, its expected normative functions and state of health as well as the fit of indicator species with the environmental features and functions present. Together, physical habitat system analysis and species habitat system analysis will help determine critical relationships within the system necessary to provide the potential for habitat at all scales. It will also identify critical features and attributes of the system at the scale of examination and will diagnose likely changes in system function and the potential response of the biota to these changes in state (Warren 1979; Frissell et al. 1986; Naiman et al. 1992). This information should help managers identify potential management strategies for protection and where necessary remediation and rehabilitation (Fig. 2, question 6).

It is not necessary to always employ both physical and species analyses. Physical system analysis can be used as a diagnostic of the relative health of operation of the physical processes and their responses at the three scales. However, this information would not be definitive in relation to how well the physical environment was meeting the needs of species within the system. The use of the species habitat system analysis using an indicator species for the system would help to not only identify the fit of the species to the physical environment, but also flag situations where a fit is expected but appears not to be realized. In those circumstances, there may be biochemical or water-quality issues that may explain the lack of fit. Although this paper does not delve into chemistry and habitat linkages, the use of the evaluative framework in a particular watershed may be useful in identifying the need to examine chemistry as the next step in management.

Figure 3 demonstrates the logic of this analysis and generates six management strategies (there may be others) that encompass protection, remediation, and rehabilitation as encouraged by the National Research Council (1992). These are a simplified list compared with proposed strategies defined by Francis et al. (1979) and Steedman and Regier (1987). We define protection as the management strategy whereby we attempt to maintain states, conditions, and forms against adverse change. Remediation strategies attempt to restore impaired conditions and forms (i.e., improve health), while rehabilitation strategies would attempt to regenerate or replace lost conditions and forms (i.e., provide integrity).

Strategies 1–3 suggest there is a natural fit between the environment and the species of interest, while strategies 4–6 suggest that the environment is not as expected even though there may be a fit for some indicator species. The management decisions inherent in strategies 4–6 are whether the indicator species present in the system is deemed acceptable or desirable (e.g., carp, *Cyprinus carpio*, in a degraded warmwater river). If so, then are managers prepared to manage the system for this fit? In cases where physical environments have been altered but are deemed to be acceptable from a management or public

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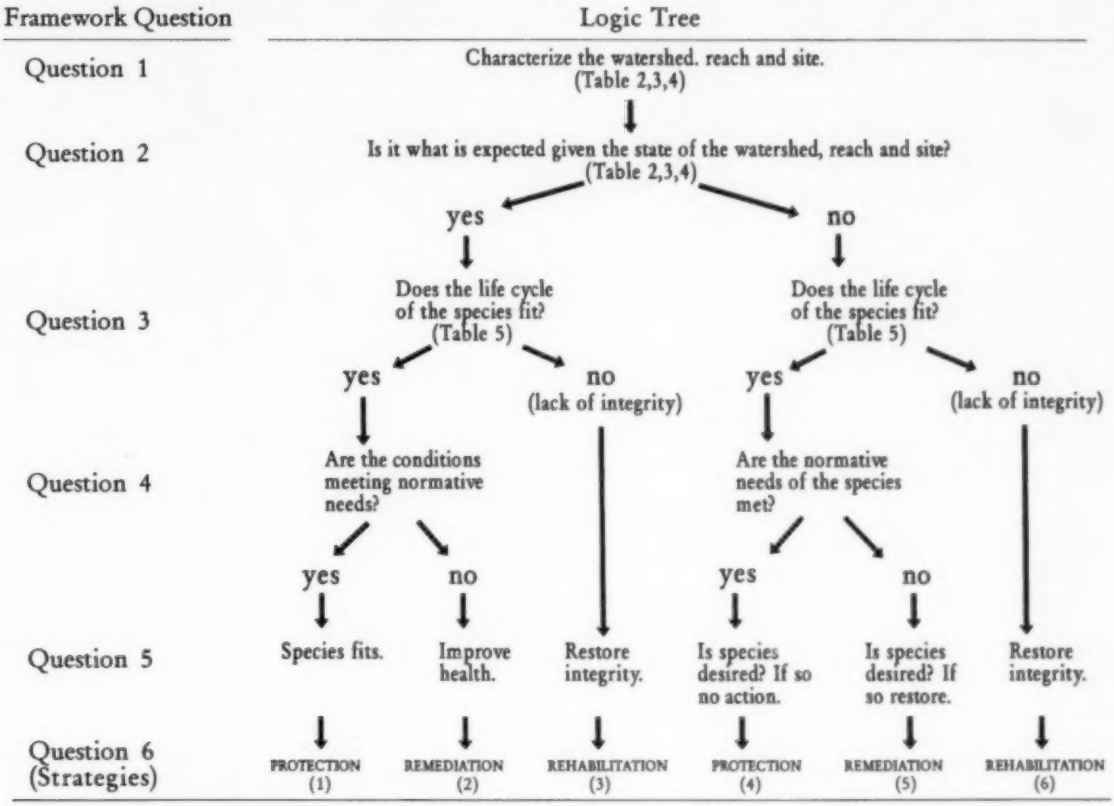
Fig. 3. A logic tree that demonstrates the application of the framework (Fig. 2) with the use of the physical and species habitat systems analyses (Fig. 1; Tables 2, 3, 4, and 5).



point of view, the management strategies would focus on the existing (i.e., acceptable) conditions rather than attempting systemic alterations back to historical and potential conditions.

Summary

Traditionally, stream-habitat management has treated the symptoms of problems rather than causes (e.g., strengthening banks to reduce erosion when the cause is increased high flow frequency not reduced bank resistance). Such responses provide temporary local solutions rather than long-term systemic solutions. What is needed is an approach to habitat management that examines both cause and response at the appropriate scales and provides for resolution of causal factors.

We suggest an evaluative framework that includes a conceptual framework relating physical and biological components of the ecosystem (Fig. 1); an indicator system that characterizes these physical and biological systems (Tables 2, 3, 4, and 5); and an ecosystem framework for analysis (Figs. 2 and 3).

In this paper the concept of fit between species and physical environment is used to link health and integrity of the system (e.g., Schaeffer and Kerster 1988; Kay 1991*b*). Where health is a problem, a population may be impaired but not necessarily eliminated. Where integrity is a problem, elimination is more likely than mere impairment. In either case the fit between the habitat system and the requirements of the species is limited.

In an aquatic system the potential fit is defined by the stable state of climate, erosional regime, and land cover in the watershed. Health and integrity are means of assessing how well the form and structure of the reaches and sites created by the flow, sediment load, and available valley slopes within watershed meet the needs of a target species. Where this occurs, habitat is available for the species, and it is probable that the population is stable, resilient, productive, and barring catastrophic events (e.g., a toxic spill), self-sustaining. An ecosystem analysis should be possible from either approach: physical environment towards life system requirements or from required biotic habitat requirements to physical environment.

From a management perspective, physical habitat system analysis is useful for determining the state and conditions that drive processes and their effects on habitat created in the system. Managers should be aware that the physical habitat system is not linear in its relation to the species habitat system. Lags in physical versus biological responses often occur. For example, several to many years can occur from the time between changes in watershed sediment discharges to adjustments to channel form and finally losses in physical living spaces (e.g., Leopold et al. 1964; Leopold 1994). Awareness of the interactions of the temporal and spatial scales is essen-

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tial to understanding and managing for cause-response relationships within watersheds.

Conclusions

The evaluative framework and model provides a means of structuring information to understand cause-response relationships between physical environment and habitat at three scales within watershed ecosystems. The framework also provides for an integrative analytical approach for examining information at three scales. The evaluative model provides diagnostic tools for determining health and integrity and, therefore, fit between species and the physical environment. This information in turn provides a watershed-based ecosystem approach to evaluation of fish habitat. This should result in a more integrated approach between physical and biological scientists and managers and a more integrated approach for the development of management strategies.

The evaluation model presented here is conceptual and, while based on a synthesis of the literature, requires testing. Further identification of appropriate indicators both in the physical analysis and the indicator species analysis is needed. In particular, a broader community-based understanding of physical habitat relationships is required.

Not included in this discussion are the biochemical processes that also influence habitat at all scales. The linkage of biophysical and biochemical interactions is also needed.

Managers must be able to determine where important habitat occurs within a watershed and ideally determine how and why changes of land use will modify habitat. Cause-response information is extremely important for input into resource and land-use planning and ecosystem restoration. Standardized methodologies exist for fish habitat assessment (e.g., Armantrout 1981; Platts et al. 1983), whereas tools to assist in determining the impact of human disturbances, scale of controlling impact, and their cause-response relationships are limited. Examples of the use of cause-response information for ecosystem based restoration is also limited and sorely needed (National Research Council 1992).

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Can trained observers accurately identify lake trout spawning habitat?

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Abstract: The ability of trained observers to accurately identify potential spawning sites of lake trout (*Salvelinus namaycush*) was tested in a 67-ha lake. Ten-metre sectors of shoreline were first visually assessed and classified by pairs of naive and expert observers. Lake trout were then displaced from their traditional spawning sites and forced to choose new sites from a 2050-m section of previously classified shoreline. Forty-one sectors from the test area were selected by the displaced fish for spawning. Egg deposition was restricted to 63 patches (0.25–5.0 m^2) of substrate (2–30 cm) within the sectors. An estimated 298–551 female lake trout used a total surface area of 53.4 m^2 for egg deposition. Observers were able to correctly classify 59–76% of the shoreline sectors containing egg patches, but their success rate was mainly because of the high number of sites they selected. The study showed that traditional assessment methods are useful for large-scale habitat mapping, but precise predictions of the location of individual spawning sites may not be possible.

Résumé : La capacité d'observateurs qualifiés à repérer avec précision les zones de fraye potentielles du touladi (*Salvelinus namaycush*) a été mise à l'essai dans un lac de 67 ha. Des paires d'observateurs respectivement néophyte et expérimenté ont d'abord évalué visuellement et classé des tronçons de 10 m de berge. Les touladis ont ensuite été éloignés de leur frayère habituelle et ainsi forcés d'en choisir une nouvelle à l'intérieur des 2050 m de berge préalablement classée. Les poissons déplacés ont établi leurs frayères dans 41 des tronçons de l'aire étudiée. A l'intérieur de ces tronçons, la ponte s'est limitée à 63 zones de 0,25 à 5,0 m5 couvertes de 2 à 30 cm de substrat. Un nombre estimatif de 298 à 551 femelles ont ainsi utilisé pour la ponte une superficie totale de 53,4 m5. Les observateurs ont été capables de classer correctement 59–76 % des tronçons de rivage renfermant des zones de ponte, mais ce taux de réussite est surtout dû au fait qu'ils avaient sélectionné un grand nombre de tronçons. La présente étude montre que les méthodes classiques d'évaluation sont utiles pour la cartographie des habitats à grande échelle. Cependant, ces méthodes ne permettent sans doute pas de prédire avec précision la position de chaque frayère.
[Traduit par la Rédaction]

Introduction

Lake trout (*Salvelinus namaycush*) in small lakes typically spawn at shallow shoreline sites in areas of clean coarse substrate (DeRoche 1969; Martin and Olver 1980; Gunn 1995; Kelso 1995). This reproductive habitat is vulnerable to infilling, sedimentation, and water drawdown that can adversely affect natural reproduction of lake trout stocks. Aquatic resource managers, therefore, need reliable methods of identifying and protecting this important habitat.

Visual surveys (usually from boats, but also by snorkelling or SCUBA diving) of shoreline features, such as substrate size and cleanliness, have often been used to identify potential spawning habitat for lake trout (Blais et al. 1984; McMurtry 1986; Nester and Poe 1987; Kelso et al. 1996) but rarely has there been an explicit test of the performance of the observers conducting the surveys.

We conducted trials to determine whether experienced ("expert") or recently trained ("naive") observers could correctly identify areas that lake trout would select for spawning. This experiment is part of a long-term study into the effect of habitat loss on recruitment by lake trout in Whitepine Lake, near Sudbury, Ont. Previous studies demonstrated that lake trout exhibit high fidelity to very specific patches of substrate (Gunn 1995). However, when denied access to traditional sites, lake trout rapidly selected and deposited eggs at alternate sites (McAughey and Gunn 1995). For example, in 1992, when 4 substrate patches that represented 15% of the embryonic habitat was removed, 12 small alternate sites were selected for spawning. In 1993, when access was denied to 50% of the traditional habitat through the removal of one more, relatively large, traditional egg deposition patch, eight more new sites were selected. These observed behavioural responses to habitat manipulation created the opportunity in 1994, of testing a priori predictions of spawning site selection, when all the historic habitat was scheduled for removal.

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Study lake

Whitepine Lake (47°17′N, 80°50′W) is a small (67-ha surface area; maximum depth 22 m; mean depth 5.6 m), headwater (elevation 412 m) single basin lake located approximately 90 km northeast of Sudbury, Ont. Our small research station is the only building within the 328-ha watershed of this remote lake. The lake is accessible only by aircraft or by a very rough seasonal road. No recreational angling has been permitted in Whitepine Lake since 1980 and experimental studies are restricted to live capture and release techniques.

A very simple fish community is currently present in Whitepine Lake. It consists of naturally reproducing lake trout, yellow perch (*Perca flavescens*), Iowa darters (*Etheostoma exile*), and a few

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Table 1. Assessment of the abundance of adult lake trout (>370 mm fork length) in Whitepine Lake for surveys conducted during May 13–25, 1992, May 3–15, 1993, and May 4–16, 1994.

(A) Mark–recapture

Year	No. marked	% Recaptured	Estimated total no.	Estimated total biomass ($kg \cdot ha^{-1}$)
1992	188	19	554 (399–765)	8.5 (6.1–11.7)
1993	262	32	547 (439–679)	7.6 (6.1–9.5)
1994	237	17	812 (595–1102)	10.4 (7.6–14.1)

(B) Index netting

		Catch per unit effort	
Year	No. of sets	No.	Weight (kg)
1992	131	1.84 (1.38–2.33)	1.65 (1.22–2.09)
1993	120	2.71 (2.14–3.28)	2.50 (1.95–3.05)
1994	120	1.90 (1.51–2.30)	1.21 (0.90–1.53)

Note: Abundance estimated by Schnabel continuous mark–recapture of angled and gillnetted fish. Total biomass estimated from measured size distribution of captured fish. Estimated total number and biomass with 95% confidence intervals (in parentheses) presented. Index netting using short duration (30 min.) sets of small mesh (38-, 58-, and 63-mm stretched mesh) gillnets was also used to assess annual changes in abundance, expressed as catch per unit effort ($no. \cdot h^{-1}$ or $weight \cdot h^{-1}$). Sample means and 95% confidence intervals (in parentheses) presented for the catch per unit effort data.

cyprinid species. Adult lake trout exhibit the small body sizes characteristic of planktivorous populations. The mean and range of fork lengths of lake trout ($n = 86$) sampled at the spawning sites in 1994 were 428 and 370–519 mm, respectively. Males and females were mature at approximately 390 mm fork length. The abundance of adults, assessed using a mark-recapture experiment (Schnabel model) and through index netting (Lester et al. 1990), are presented in Table 1. Population estimates were conducted in the spring when water temperatures were 6–15°C. Estimates of the adult population abundance were based on fish greater than 370 mm rather than 390 mm to account for the seasonal growth rate of 20 mm (back calculated from scale readings) for young fish (age 5+ and 6+) in their first year of maturity in this population. These results indicate that adult lake trout abundance (554–812) and biomass (8.5–10.4 $kg \cdot ha^{-1}$) have been relatively stable (i.e., overlapping 95% CI) in Whitepine Lake during the period when habitat manipulation experiments were conducted (Table 1).

The traditional spawning areas of lake trout in Whitepine Lake are along the south and east shorelines in water depths of <2 m (Liimatainen et al. 1987; Gunn 1995; McAughey and Gunn 1995). Before any manipulations of habitat began in 1992, there were three traditional areas where adults congregated to spawn (Fig. 1). Egg deposition was not random in these areas, but was concentrated over patches of small substrate, with highest deposition (877–9027 $eggs \cdot m^{-2}$) occurring in the smallest size category (2–10 cm) (Gunn 1995; J.M. Gunn, unpublished data). These patches are usually visible during the spawning period because of the cleaning action of spawning fish milling over the substrate. Prior to the spawning season the egg deposition patches are not easy to recognize because the substrate is covered with a fine coating of detritus or algae. The total surface area of the substrate patches that made up the traditional spawning habitat at the start of the manipulation experiment in 1991 was approximately 41 m^2. No other areas of spawning activity or sites of egg deposition had been observed during the previous 12 years of assessment work on Whitepine Lake (Gunn and Keller 1984; J.M. Gunn, unpublished data).

Methods

The classification of shoreline sectors by naive and expert observers occurred in late summer before lake trout entered the nearshore areas to spawn. Therefore, observers could not use the presence of fish or the appearance of freshly cleaned sites to detect potential spawning sites.

Naive observers were trained to recognize lake trout spawning habitat by first studying the physical appearance of traditional spawning sites on Whitepine Lake (training duration approximately 15 min). They were then instructed to locate similar sites along a 2050-m transect of shoreline that had been marked at 10-m intervals. The transect extended from shore to approximately 2 m depth to encompass the area of lake bottom with coarse substrate (at greater depths most coarse substrate in this small lake is heavily infilled with organic or inorganic sediment). With the exception of an approximately 30-m section of shoreline in the northwest corner of the lake, and a small mid-lake shoal, the transect contained all of the coarse substrate in the lake.

The naive observers were instructed to look for sectors that contained even very small patches (≥0.20 m^2 in surface area) of suitable size substrate (2–20 cm diameter) if they were free of heavy sediment coatings or infilling. The resolution of the classification scheme was, therefore, a 10-m length of shoreline (i.e., the presence of a single substrate patch would be sufficient to classify a 10-m sector as a "potential spawning site"). Two naive observers carried out their classification of each of the 205 shoreline sectors between 07:00 and 10:00 when the lake surface was calm and substrate could be clearly seen. Naive observers took approximately 90 min to cruise the shoreline by boat while conducting the sector classifications. Sector classification was conducted independently by observers and repeated the next day. The transect was run from the opposite direction during the second inspection without having access to previous data.

"Experts" were individuals with several years of experience with lake trout spawning assessment. The two experts used in this study also had 2 or more years of prior experience watching lake trout spawn in Whitepine Lake. The experts conducted the training of naive observers, but rather than use the usual shoreline cruising method (by boat) of locating potential spawning habitat they attempted to more precisely locate useable spawning sites along the marked transect by swimming with mask and snorkel. This method permitted closer examination of additional features (e.g., substrate interstitial depth, site topography) reported to be associated with lake trout spawning sites in other lakes (Marsden and Krueger 1991; Fitzsimons 1996). Each expert did one independent assessment of the 205 sectors.

Habitat removal

To test the accuracy of the observers' classification, lake trout were

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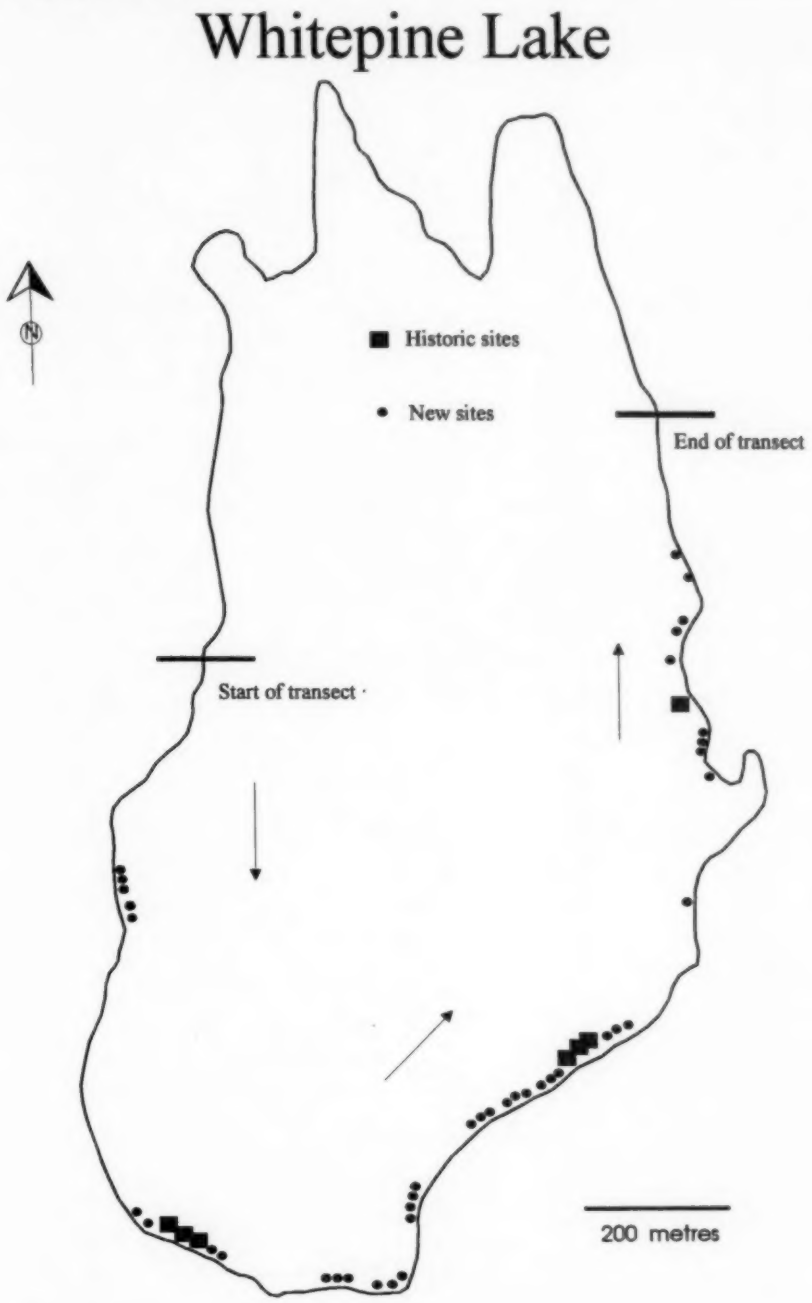
Fig. 1. Whitepine Lake showing location of the 2050-m shoreline transect, the traditional spawning sites, and the 41 new sites selected by the lake trout after the traditional sites were removed in 1994. Each illustrated site is a 10-m section of shoreline that contains a least one patch of substrate where egg deposition occurred.



displaced from their traditional sectors and forced to select new sites. This manipulation was conducted by covering spawning substrate with plastic tarpaulins approximately 2 wk prior to the expected period of spawning (McAughey and Gunn 1996). Seven whole 10-m sectors of shoreline were covered out to a depth of approximately 2 m to eliminate access to all traditional patches of spawning substrate (Fig. 1). With the removal of the traditional sites the number of sectors with potential spawning habitat on the transect was reduced to 198.

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Table 2. Performance of naive (N1, N2) and expert (E1, E2) observers at classifying lake trout spawning sectors from a 198 sector experimental transect in Whitepine Lake, 1994.

		Sectors selected		Classified correctly		Sample weighted success rate[c]
	Observer type	N_s[a]	%	N_c[b]	%	($N_c/N_s \times 0.207$)
Trial 1	N1	101	51.0	31	30.7	1.5
	N2	72	36.4	30	41.7	2.0
Trial 2	N1	124	62.6	36	29.0	1.4
	N2	88	44.4	28	31.8	1.5
Trial 3	E1	53	26.8	24	45.3	2.2
	E2	55	27.8	26	47.3	2.3

Note: Performance was measured in terms of how many of the 41 actual spawning sectors were correctly indentified by the observers.

[a]Number of sectors selected.

[b]Number of sectors classified correctly.

[c]Each site had a probability of 0.207 of being correctly classified by observers by chance alone given that the lake trout selected 41 of the 198 sectors for spawning.

Spawning observations

Selection of spawning habitat by the displaced fish was determined during 13 days of nighttime observations during October 3–20, 1994. A random design (four start points; two directions) was used to search for lake trout along the entire 3.86-km perimeter of the lake. Floodlights were used to locate and count fish as observers slowly motored or drifted through each sector. This assessment method usually scared fish off a site, but prior experince has shown us that they move back to a selected substrate patch within a few minutes of the boat passing by. When spawning appeared to be complete (i.e., nightly shoreline congregations of adult fish had dispersed), egg deposition was confirmed by a diver who carefully inspected all areas containing coarse substrate. Particular attention was given to searching for eggs within the substrate at sites where adult lake trout were observed. When a patch of eggs was discovered, we measured surface area of the patch, water depth, distance from shore, and substrate size.

Results

Single fish were seen outside the transect, but no sites of repeated use by adult lake trout or with egg deposition were found, confirming our initial hypothesis that the transect encompassed all of the spawning habitat in the lake. Within the transect adult lake trout were observed within 43 sectors. The maximum number of fish observed in a sector ranged from 4 to 41. During the peak of spawning activity (Oct. 5–12), the total number of fish counted during a search along of the lake perimeter ranged from 179 to 195. Such counts were considered rough estimates because of the difficulty of counting fish at night, but the survey did reveal that adult lake trout were using a large number of very specific sites. Sites were used night after night, supporting our initial assumption that the shoreline cruising and spotlight method was not seriously disturbing spawning activity. No attempt was made to determine whether individual fish were displaying site fidelity.

Egg deposition occurred in 41 or 20.7% of the sectors (Fig. 1). The sectors selected for spawning had a total surface area of 3126 m^2 (16.1% of transect total); however, most spawning sectors had extensive areas of bedrock, steep rock faces, or unsuitable substrate (sand, silt, detritus). Egg deposition was, therefore, extremely patchy within a sector and was frequently confined to tiny ledges or other small isolated areas of usable substrate. A total of 63 egg-containing substrate patches that ranged in surface area from 0.25 to 5 m^2 (median 0.5 m^2) were identified. The total surface area of the egg deposition patches in the lake was 53.4 m^2. Water depth over the areas of egg deposition ranged from 15 to 196 cm (median 30 cm) and these patches were from 0 to 4.0 m from shore (median 1.0 m). Substrate in the egg deposition patches ranged from 2 to 30 cm in diameter. Based on the calculated egg production of the population, using the 1994 mark-recapture estimate of the biomass of adult females (255–472 kg; Table 1), and a fecundity of 1600 eggs·kg^{-1} (Payne et al. 1990), the estimated egg deposition rate was 7640 – 14 143 eggs·m^{-2} within the egg deposition patches.

Performance of observers

On their first pass through the transect, the naive observers classified 72–101 sectors (36–51% of transect total) as potential spawning sites. The observers were successful at identifying 30–31 (73–76%) of the 41 sectors that the lake trout later chose for spawning (Table 2), but their success appeared to be mainly because of the high number of sites they classified as potential spawning sites. Chance alone could have accounted for 15–21 (50–68%) of the sites correctly classified (Table 2). The naive observers also displayed considerable individual variability, agreeing on only 23 sectors where the fish later spawned. During the second trial, both naive observers increased the number of selected sectors, but did not increase their success rate (Table 2).

The experts correctly identified 24–26 of the 41 sites where lake trout spawned (Table 2). They exhibited a higher success rate than the naive observers, but because they chose fewer sectors, they were actually less successful in locating spawning sites than the less experienced observers. Fifteen to 17 sites were missed by the experts as compared with 9 or 10 by the naive observers. The experts also showed high individual variability. They agreed on their classification for only 19 of the sites where spawning occurred.

Discussion

There are two principal findings for lake managers from this study. The first is that managers can still continue to use rather general rules and procedures to map shoreline areas and be successful at describing the useable spawning habitat for lake trout. For example, the initial selection of the transect area in Whitepine Lake, based on the presence of clean coarse sub-

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strate was sufficient to capture all of the sites where spawning occurred. Such areas can be readily mapped during rapid inspection of the shoreline and may perhaps be successfully mapped using aerial photographs on some clear lakes. With this level of general information managers can design shoreline development plans that minimize the risk of disturbance of spawning habitat for this species.

The second lesson is that managers must err on the side of caution when considering any shoreline development where useable spawning habitat exists. Our study shows that it is very difficult to predict the precise location of spawning sites within these generalized areas. The success rate of the trained observers was only about 1.4–2.3 times better than random selection alone would have produced. Predicting the location of spawning sites on a larger lake, or one with fewer active sites, would no doubt have been much more difficult than on Whitepine Lake.

Some improvement in the site classifications on Whitepine Lake may have occurred if we had used broader habitat descriptions from surveys of spawning sites on a variety of lakes (e.g., Martin and Olver 1980; McMurtry 1986; Gunn 1995). In our study there were three spawning sites that all four observers missed. These sites differed from the other selected sites in that they were either further offshore or slightly deeper, or contained larger substrate, suggesting that all observers were using criteria or survey methods that were not broad enough to capture all sites.

These results support our earlier finding (McAughey and Gunn 1995) that lake trout respond rapidly to the loss of habitat by selecting alternate spawning sites. However, the results do not prove that unlimited amounts of embryonic habitat exist in the study lake, or that the loss of traditional sites will not affect recruitment. Lake trout were able to find approximately the same amount (surface area) of habitat after they were displaced from their traditional sites, but we do not know if the same number of young will be produced from these sites. Indeed, even though 63 alternate substrate patches were found, egg density was very high. The estimated egg densities for 1994 (7600–14 000 eggs·m^{-2}) are realistic (i.e., within the range of sampled deposition in this lake (maximum 9027 eggs·m^{-2}; Gunn 1995)), but are much higher than those reported from other studies. Fitzsimons (1995) reported a maximum of 11 649 eggs·m^{-2} at an artificial site in Lake Ontario, but only a very few natural spawning sites described in the literature have egg densities over 1000 eggs·m^{-2} (Martin 1957; Booth et al. 1993; Perkins and Kreuger 1994) and most sites are usually in the 20–500 egg·m^{-2} range (Martin and Olver 1980; Fitzsimons 1995; Kelso et al. 1995). The high density of egg deposition on Whitepine Lake and the multitude of tiny sites may, therefore, actually indicate that the resident population has rather restricted choices for appropriate places to deposit eggs.

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A hierarchical approach to assessing habitat suitability and yield potential of lake trout

Terry R. Marshall

Abstract: Ecological properties essential for the survival and production of a lake trout (*Salvelinus namaycush*) population can be placed in a hierarchical framework. Prior to any consideration of yield potential, it must be determined that the lake is capable of supporting a self-sustaining lake trout population, with surplus production available for a fishery. The steps required to perform this assessment and determine yield expectations are outlined. Initially, the lake is plotted along a continuum of mean depth and primary productivity to evaluate whether the critical temperature and oxygen requirements of lake trout are met. A review of other physical habitat attributes essential for the success of the population follows, such as the availability of spawning substrate and nursery refugia. If the fundamental environmental and physical habitat needs are met, a viable lake trout population could be expected, and an evaluation of harvest potential is appropriate. An estimate is made first of total community yield, then of the sustainable harvest of lake trout alone, applying thermal habitat volume and lake area models. Finally, adjustments are made to this estimate through consideration of modifiers that may constrain lake trout production, including community biodiversity and various anthropogenic stressors. Small lakes (<1000 ha) are most affected by these constraints.

Résumé : Les propriétés écologiques essentielles à la survie et à la production d'une population de touladi (*Salvelinus namaycush*) peuvent être hiérarchisées. Avant de chercher à connaître le rendement potentiel de cette population, il faut vérifier si le lac peut permettre à celle-ci de se maintenir d'elle-même et de produire un surplus exploitable. Nous décrivons les étapes que nécessitent cette évaluation et les prévisions de rendement. Il faut d'abord marquer chaque lac sur un plan de coordonnées correspondant respectivement à la profondeur moyenne et à la productivité primaire, afin de déterminer si le lac satisfait aux exigences critiques du touladi en matière de température et d'oxygène dissous. On examine ensuite les autres propriétés physiques de l'habitat qui sont essentielles au succès de la population, comme la présence de substrats convenant à la fraye et de lieux propices à l'alevinage. Si les exigences fondamentales en matière d'environnement et de milieu physique sont satisfaites, on peut s'attendre à obtenir une population viable de touladi, et il y a lieu d'évaluer le potentiel de récolte. On fait d'abord une estimation du rendement total de la communauté, puis on évalue le taux d'exploitation durable du touladi, en utilisant des modèles axés sur le volume d'eau de température adéquate et la superficie du lac. Finalement, on rajuste cette estimation en fonction des autres facteurs pouvant restreindre la production de touladi, comme la biodiversité de la communauté et les diverses sources anthropiques de stress. Les petits lacs (moins de 1000 ha) sont les plus touchés par ces contraintes.
[Traduit par la Rédaction]

Introduction

The long-term survival of a fish population is dependant on the quality of ambient environmental conditions, which, when described in terms of the critical needs of the species, defines their fundamental niche envelope (Fry 1947; Kerr and Ryder 1977; Magnuson et al. 1979). When these conditions are met, the productive capacity of the population is largely a function of the quantity of this multidimensional resource space, as measured along an areal or volumetric axis (Christie and Regier 1988). At a finer scale, the suitability of physical habitat features can further influence production, as can the complex of interactions with other species (Marcus et al. 1984; Colby et al. 1987; Carl et al. 1990). Together, these attributes define the realized niche for the species, as constrained within its fundamental niche envelope.

Ryder and Kerr (1989) proposed that a hierarchic framework be used to assess habitat rehabilitation needs for any fish species. They argued that the key survival determinants (identified as dissolved oxygen, water temperature, subsurface light, and dissolved nutrients) must receive primary attention; following this, the limiting effect of physical habitat and other factors should be considered. Sly and Busch (1992) examined the use of hierarchical scales for determining the productive capacity of aquatic habitat. They contended that while large-scale low-resolution data (i.e., broad environmental characteristics) are essential for setting harvest estimates, a complimentary set of small-scale high-resolution data (i.e., site-specific physical data, community structure, etc.) is required to identify conditions which may limit or enhance productive capacity.

In this paper, a hierarchical approach is proposed through which to assess a lake's potential to support a self-sustaining lake trout (*Salvelinus namaycush*) population, and to determine the potential yield of this species to a fishery. This is a three-phase process, with two steps involved in each phase

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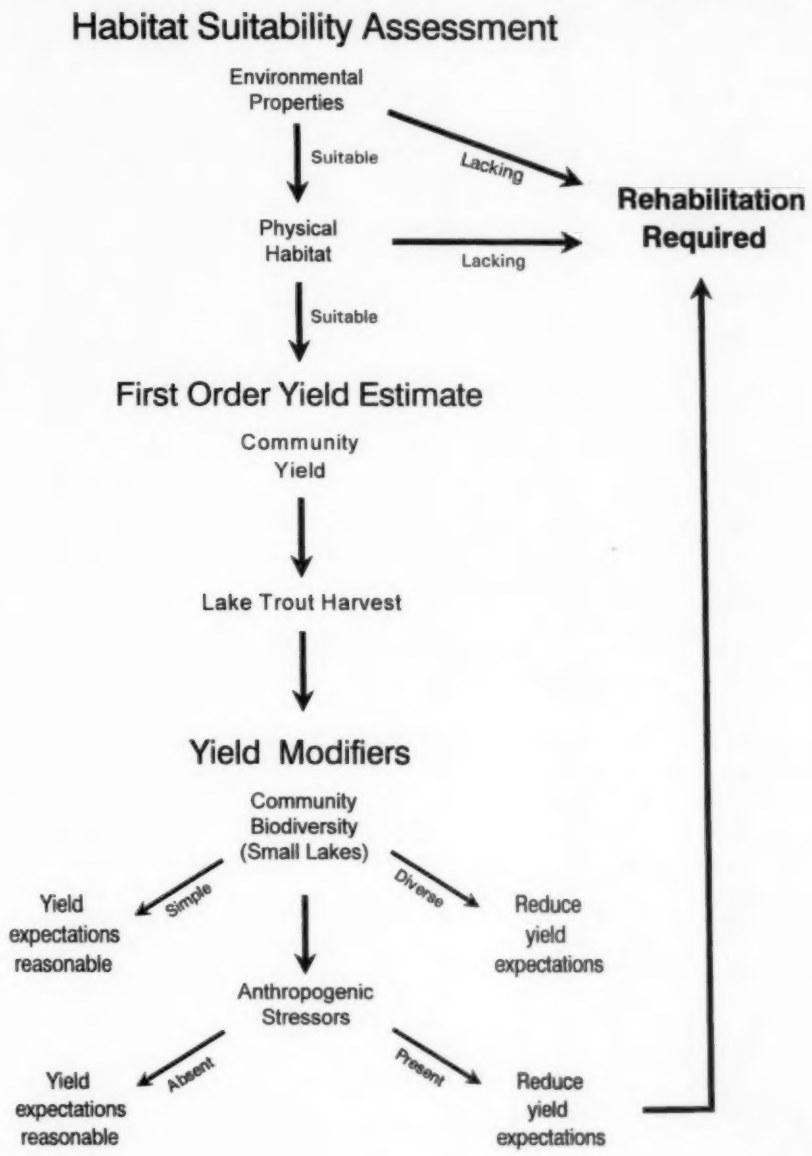
Fig. 1. Flowchart illustrating the hierarchy of steps required to properly evaluate the habitat suitability of lake trout and assess their yield potential.



(Fig. 1). Initially, an assessment of habitat suitability is undertaken, and the key environmental parameters critical to lake trout survival are compared with known thresholds. If the environment is deemed suitable in this respect, physical attributes essential for the success of the species, such as the availability of spawning and nursery habitat, are then examined.

If it is determined that the lake is capable of supporting a viable lake trout population, and that surplus production may be available to a fishery, the second phase of the process is activated. A first-order yield estimate is made for the entire fish community, then harvest models are applied that are specific for lake trout. In the last phase, yield estimates are adjusted through consideration of yield "modifiers" that may affect energy flow to lake trout and their rates of survival at various life stages. A lake set assembled by Payne et al. (1990) is used to demonstrate aspects of this approach (Table 1).

Habitat suitability assessment

Environmental properties

The lake trout is a stenothermic species, dependent on a supply

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Table 1. Data used for the demonstration of environmental suitability and yield estimation, as compiled by Payne et al. (1990).

Lake	Area (ha)	Mean depth (m)	Thermal habitat volume (hm^3)	Secchi depth (m)	No. of fish species	Harvest ($kg \cdot yr^{-1}$)	Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)
Superior	8 241 400	148.0	1 011 766	30.0	67	1 895 500	0.23
Michigan	5 801 600	84.6	471 483	15.6	114	3 248 900	0.56
Huron	4 165 900	67.0	264 505	10.4	99	1 499 700	0.36
Great Slave	2 538 200	62.0	114 102	7.1	26	1 003 200	0.40
Ontario	1 947 700	84.0	118 290	4.2	112	311 600	0.16
Georgian Bay (L. Huron)	1 375 200	51.0	102 290	10.4	99	660 100	0.48
Erie	623 700	24.3	19 822	3.6	113	50 000	0.08
Reindeer	556 900	17.0	25 866	7.0	22	278 600	0.50
North Channel (L. Huron)	455 000	22.0	21 672	10.4	99	254 800	0.56
Nipigon	448 100	54.9	24 638	6.5	45	130 900	0.29
Wollaston	206 200	20.6	11 785	6.8	20	159 200	0.77
La Ronge	130 700	13.5	2865	4.5	23	64 000	0.49
Cree	115 200	14.9	4472	7.8	16	100 600	0.87
Amisk	32 100	13.1	895	3.8	21	13 400	0.42
Opeongo	5894	14.6	112	5.8	26	4005	0.68
Chiblow/Denman	2675	23.9	62	7.8	11	1570	0.59
Flack	951	19.9	27	11.2	13	1285	1.35
Bone	121	7.7	0.8	5.5	13	256	2.12
Christman	59	7.0	0.5	6.3	4	94	1.59

Note: Lake trout harvest values for the first 14 lakes represent the maximum 15-year running average annual commercial harvest. Harvest values for the remaining five lakes represent the average annual angling catch, recorded over a 12- to 17-year period with moderate to heavy fishing pressure. Harvest, fishing effort, total mortality rate, and growth of lake trout were stable throughout this period. The number of fish species are from distributional lists compiled by Ryder (1972), Anonymous (1991), and from unpublished reports of the Ontario Ministry of Natural Resources. Lake of the Woods was removed from the original Payne et al. (1990) lake set, as it is doubtful that commercial catch data for this lake would truly reflect maximum sustainable yield for lake trout. Commercial fishing was never allowed in Whitefish Bay, the deepest part of the lake and the area considered to support most of the lake trout production (T. Mosindy, Ontario Ministry of Natural Resources, Kenora, Ont., personal communication).

of cold, well-oxygenated water for their long-term survival (Martin and Olver 1980). Following a review of the literature, MacLean et al. (1990) suggested that an upper temperature limit of 15.5°C and a lower dissolved oxygen limit of 4 $mg \cdot L^{-1}$ be considered useable habitat for lake trout. Similarly, values of 10°C and 6.0 $mg \cdot L^{-1}$ represent optimal habitat, defined as that stress-free volume where neither temperature or oxygen is limiting. They proposed that, on a volume basis, 20% optimal habitat and 40% useable habitat represents incipient limiting conditions below which lake trout reproductive potential and abundance would be constrained.

Marshall and Ryan (1987) observed that, in northwestern Ontario, the proportional abundance of lake trout in gillnet catches varied along a continuum of lake mean depth and Secchi depth, falling to near zero at values of less than 6.3 or 4.0 m, respectively. Lake depth is an important environmental variable for lake trout, as it governs not only the thermal regime but also the quantity of dissolved oxygen stored at the time of stratification (Cornett and Rigler 1979; Walker 1979; Cornett 1989). Secchi depth is highly correlated with primary production, as are other trophic indices such as phosphorus concentration and chlorophyll *a* concentration (Carlson 1977; Walker 1979). There is a direct relationship between primary production and the rate of hypolimnetic oxygen depletion (Lasenby 1975; Charlton 1980; Cornett and Rigler 1980), which determines the late summer oxygen supply for lake trout.

Ryan and Marshall (1994) developed a set of models that combine a measure of primary productivity (phosphorus, chlorophyll *a*, or Secchi depth) with lake mean depth to predict the seasonal oxygen depletion in lakes. They observed that lake trout seldom occurred in lakes in which the seasonal oxygen reserves were depleted by 40% or more. They considered this a niche boundary, as lakes that plotted beyond this point (i.e., >40% oxygen depletion) apparently did not provide the thermal and oxygen conditions necessary for long-term survival of lake trout populations. This boundary would likely parallel the optimal habitat dimensions identified by MacLean et al. (1990). The Ryan and Marshall (1994) models, with their minimal data requirements, provide a means of rapidly assessing a lake environment for its suitability for lake trout. To illustrate this process, the lake trout lakes from Table 1 were mapped onto axes of Secchi depth versus mean depth, with the 40% oxygen depletion isopleth of Ryan and Marshall (1994) overlain (Fig. 2).

As might be expected based on their historic sustained lake trout fisheries, all lakes fall above the niche boundary for this species. Some lakes fall between the 20% and 40% oxygen depletion isopleth, however, indicating their more sensitive nature, where small increases in nutrient loading or changes in the thermal regime may be sufficient to modify the environment to one no longer optimal for lake trout. An ever increasing risk of extinction of lake trout populations would be expected as lakes plot close to or below the 40% oxygen depletion isopleth (Ryan and Marshall 1994). The volume of habitable water would be severely constrained, leading to a reduction in population fitness and increased rates of juvenile mortality resulting from a loss of nursery refugia (Evans et al. 1991*a*). It is expected that these lake trout populations would be less resilient than those in lakes falling well above the 40%

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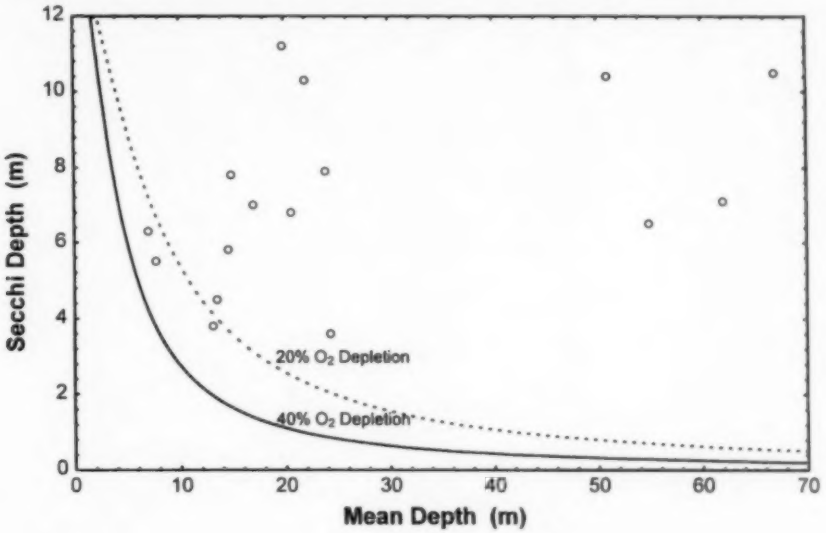
Fig. 2. The distribution of lake trout lakes along axes of mean depth and Secchi depth (excluding the three deepest lakes which exceed the scale). The solid line represents the point at which 40% of the hypolimnetic oxygen reserves would be depleted by summer's end (Ryan and Marshall 1994). This is designated a niche boundary, as lakes falling beyond this line seldom support natural lake trout populations. This boundary can also be modelled along axes of mean depth versus phosphorus or chlorophyll *a* concentration.



oxygen depletion isopleth, and would be in greater danger of population collapse triggered by other exogenous stress.

Lake trout have infrequently been reported in lakes that fall beyond the niche boundary (i.e., >40% oxygen depletion). Snucins and Gunn (1995) examined one such lake and found that while oxygen concentrations were not a concern (the water depth was sufficiently shallow to allow continuous mixing throughout the summer), bottom temperatures ranged from 15 to 20°C, well above the preferenda for lake trout during late summer. Large lake trout frequently used a shallow, cooler groundwater intrusion as a refugium, congregating at this location to avoid the inhospitable thermal conditions present elsewhere. The extreme sensitivity of this type of lake must be noted, as population sizes are normally small, enhancing the risk associated with exploitation. Any disturbance within the watershed that would affect the groundwater supply, such as timber harvesting, road building, or pipeline construction, could have a major impact on the survival of lake trout within these atypical systems.

Physical habitat

Even if environmental conditions are suitable for lake trout, their well-being is dependant on other critical attributes of physical habitat. In particular, appropriate substrate must be available for spawning and egg incubation (Gunn 1995). Lake trout are very selective in their choice of spawning sites, commonly choosing clean, well-washed, broken rubble ranging from 3 to 15 cm in diameter (Martin 1955; Martin and Olver 1980; Sly and Widmer 1984). Such material allows infiltration of eggs into interstitial spaces, ensures adequate gas exchange across cell membranes, protects eggs from mechanical buffeting, and reduces risk of predation of the developing eggs (Martin and Olver 1980; Sly 1988). The availability of such substrate is a key determinant of reproductive success and survival of early life stages.

The depth of spawning sites increases with lake size, presumably because the waves associated with a longer fetch have a deeper cleansing function (Martin and Olver 1980). In small inland Ontario lakes, spawning sites range in depth from 0.1 to 5.0 m, usually near steep dropoffs, in areas with high exposure to prevailing winds and wind driven currents. MacLean et al. (1990) developed a key to identify potential lake trout spawning locations. Classification rules were defined by summarizing observed conditions at known spawning sites, in terms of water depth, distance from shore and inlets, fetch, wind orientation, and substrate texture. Potential spawning areas can be mapped using this technique, although field inspections are required to confirm actual use by lake trout.

There is evidence that if spawning substrate is not limited, lake trout will readily select alternate spawning areas if prevented from using historic sites (McAughey and Gunn 1995). However, spawning habitat meeting the required specifications is often limited in small lakes, with only one or two spawning sites used. Such lakes are vulnerable to substrate removal or physical modifications of shorelines or water level changes that may eliminate or restrict the use of this critical spawning habitat (Evans et al. 1991*b*). If not immediately reclaimed, loss of this habitat may result in the extirpation of lake trout stocks.

First-order yield estimate

Community yield

If the habitat assessment indicates that the lake is environmentally capable of supporting lake trout, and that excess production may be available for a fishery, the next step would be the estimation of potential yield. A variety of empirical models

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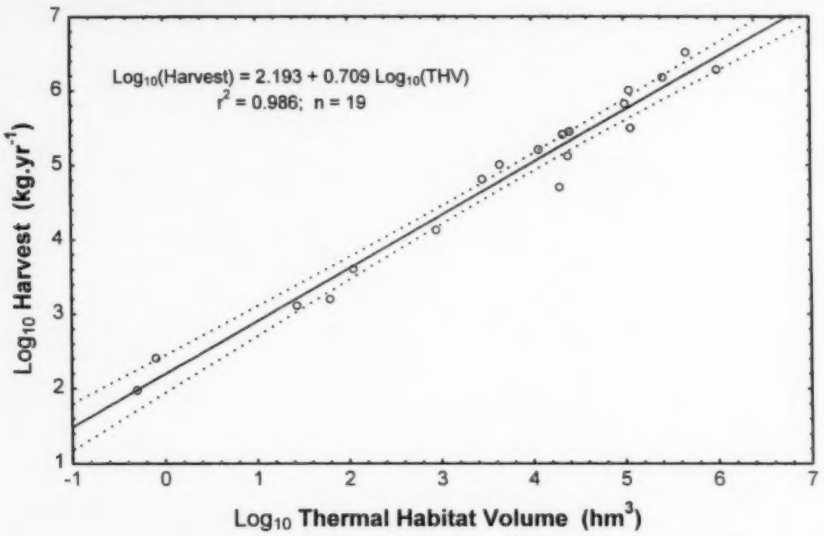
Fig. 3. The relationship between annual sustained lake trout harvest and July thermal habitat volume, modified slightly from that of Payne et al. (1990). The dotted lines represent the 95% confidence interval.



have been developed through which total yield can be predicted (see Leach et al. 1987 for a review). Data requirements are minimal for some models, requiring only a value for the morphoedaphic index (Ryder 1965), total phosphorus (Oglesby 1977; Hanson and Leggett 1982), or chlorophyll *a* (Jones and Hoyer 1982). Other models are more data intensive, requiring estimates of benthos biomass (Matuszek 1978) or production at lower trophic levels (Borgmann 1982). Total community yield should be predicted using as many techniques as data allow, rather than relying on a single model. The results may then be evaluated to determine realistic expectations.

Lake trout harvest

For any species, a measure of available living space would be expected to be closely linked to standing stock and, ultimately, to harvest potential. This concept is implicit in the thermal habitat volume (THV) model of Christie and Regier (1988), which relates fish harvest to lake thermal provisions. The THV for lake trout defines the volume of water bounded by the 8 and 12°C temperature isotherms, averaged over the summer (June–September) period. Payne et al. (1990) reanalyzed Christie and Regier's (1988) data and found that a THV calculated over a restricted midsummer period increased the precision of the model and required less field data. They recommended that the geometric mean of available July temperature profiles be used for this purpose, and documented the process required to generate a July THV. A strong relationship is evident when lake trout harvest is regressed against July THV (Fig. 3).

Lake area is also a good predictor of lake trout harvest (Fig. 4), as expected, since as lakes increase in size, so does their depth and THV. The lake area model requires map data only, and explains nearly as much of the variance in harvest as does THV (97.0% versus 98.6%, respectively). Evans et al. (1991*a*) analyzed creel data from 43 Ontario lakes (maximum 10 000 ha) and described a lake trout harvest – lake area relationship with a similar intercept (at 10 ha), but with a lower slope (i.e., $\log_{10}(\text{harvest}) = 0.60 + 0.72 \log_{10}(\text{area})$). However, they did not consider the harvest data to represent maximum sustainable yield, as it frequently represented a single survey year and included lakes with both stocked and unstocked populations.

The high correlations of these models may be somewhat misleading because of the extremely wide range of scale values. The total harvest of lake trout, lake area, and July THV range over four, five, and six orders of magnitude, respectively. When considered at any given value of lake area or THV, the 95% confidence limits of harvest indicate considerable variability. Across this interval, harvest varies by a minimum factor of 1.7 (16 293–27 479 kg·yr^{-1}) at the midpoint of the THV scale (1000 hm^3), and a maximum factor of 2.9 (96–275 kg·yr^{-1}) near the low end of the THV scale (1 hm^3). Nevertheless, both of these models represent valuable first-order predictors of lake trout harvest, and their use is recommended.

It must be emphasized, though, that the models were developed from relatively productive lakes and predict maximum potential harvest. These estimates must be fine tuned based on knowledge of other lake-specific controls on production. In lakes with few species, the lake trout yield estimates would be expected to approach (but never exceed) total community yield. In lakes supporting a diverse fish community, the difference between community yield and lake trout yield would represent that portion of the total yield which may be allocated to other fish species.

Yield modifiers

Community biodiversity

The slope of the harvest – lake area regression is less than 1.0, revealing that per unit area, small lakes would have a propor-

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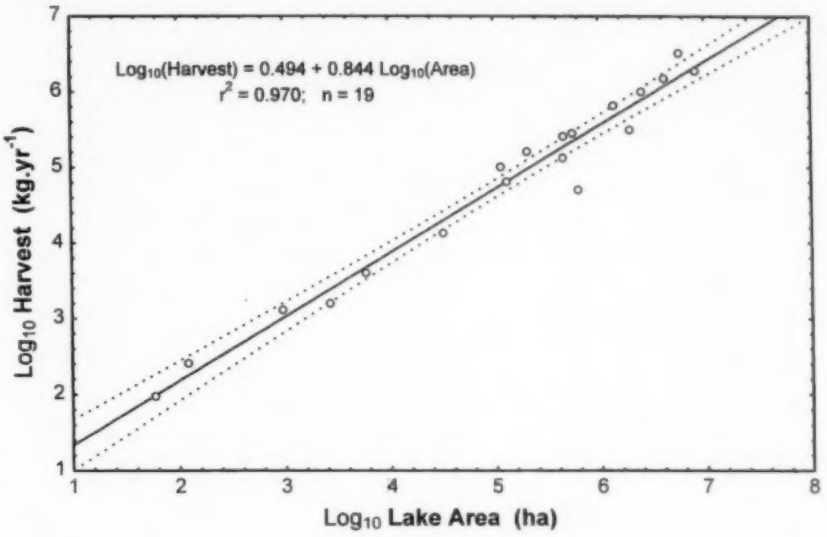
Fig. 4. The relationship between annual sustained lake trout harvest and lake surface area. The dotted lines represent the 95% confidence interval.



tionately greater lake trout harvest than larger lakes. This is consistent with the previously noted inverse relationship between lake trout yield and lake area (Goddard et al. 1987; Carl et al. 1990; Payne et al. 1990; Evans et al. 1991a). When lake area is considered over five orders of magnitude, it explains 53% of the variation in annual lake trout yield (Fig. 5). Lakes less than 1000 ha in area have a mean lake trout yield of 1.69 $kg \cdot ha^{-1} \cdot yr^{-1}$, compared with 0.46 $kg \cdot ha^{-1} \cdot yr^{-1}$ for larger lakes.

A reduction in fish yield with increasing lake area has been reported earlier by Rounsefell (1946), Carlander (1977), Oglesby (1977), and others. Ryder (1982) reasoned that this was a consequence of the proportionately longer length of shoreline per unit area in smaller lakes. This greater shoreline length would result in more littoral area to accept allochthonous inputs and provide nutrient exchange with the sediments, thereby increasing production.

Large lakes have more fish species (Barbour and Brown 1974; Matuszek and Beggs 1988), and this too may have some bearing on lake trout dynamics. Carl et al. (1990) analyzed gillnet data and reported that the greatest proportional abundances of lake trout occurred in small, deep lakes with highly transparent water and few fish species. They also examined angling creel data and found a negative correlation between species richness and lake trout harvest, after the effects of fishing effort and surface area were accounted for. Similarly, a negative relationship between lake trout yield and fish species diversity is evident for the data presented here (Fig. 6), with the fit being similar to that noted for the yield-area regression.

Trophodynamic theory suggests that this relationship could be food-web related, reflecting the availability and type of prey, and the degree of competition for these prey items. However, Kerr and Martin (1970) examined both planktivorous and piscivorous lake trout populations, and reported that the length of the food chain did not influence their yield. Similarly, Goddard et al. (1987) found that no significant difference in lake trout harvest could be attributed to food resources or the presence-absence of select species associations, after controlling for covariance with effort and surface area. However, Carl et al. (1990) found that the presence of additional piscivorous species was marginally related (negatively) to lake trout angling harvest (by number) and strongly related to lake trout relative abundance (gillnet CUE, by weight). In particular, a lower relative abundance of lake trout occurred in lakes where burbot (*Lota lota*), northern pike (*Esox lucius*), or coregonines were present.

Carl et al. (1990) noted that relatively large standing stocks of lake trout may exist in lakes without coregonines, and that lake trout yields from many of these lakes are high. These lakes often support the large invertebrate, *Mysis relicta*, which provide a higher energy content per unit food particle than do smaller zooplankton. Carl et al. (1990) argued that because of reduced trophic transfer costs, production of lake trout would be greater for populations feeding on these large invertebrates than it would be for piscivorous populations. Other studies have demonstrated increases in growth or yield of lake trout following the introduction of *Mysis* (Nesler and Bergersen 1991; Richards et al. 1991), or when comparing lakes with natural *Mysis* populations with those without (Langeland et al. 1991). Therefore, the inverse relationship between species richness and lake trout yield may reflect differences in bioenergetics, which would be especially evident between lakes with and without fish prey.

The three smallest lakes used to develop the lake trout yield models (all less than 1000) have low fish diversity and support planktivorous lake trout populations. In such lakes, lake trout would be expected to be more abundant and of smaller mean size than in larger lakes (Kerr and Martin 1970; Carl et al. 1990). In contrast, small lakes that support diverse fish communities tend to have piscivorous populations of lake trout comprised of fewer and larger individuals, and may be unable

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Fig. 5. The relationship between sustained yield of lake trout and lake surface area. The dotted lines represent the 95% confidence interval.

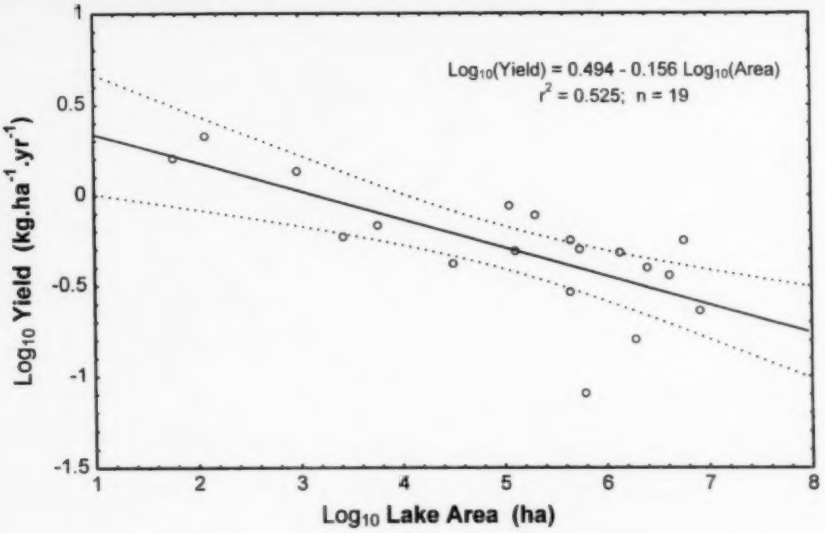
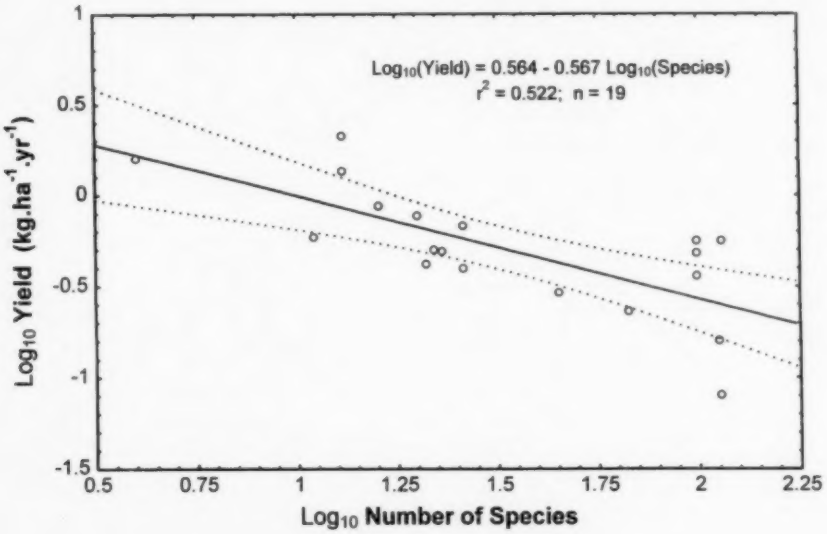


Fig. 6. The relationship between sustained yield of lake trout and the total number of fish species. The dotted lines represent the 95% confidence interval.



to provide as great a harvest as that predicted using the lake area or THV model. Similarly, the models may overestimate harvest for planktivorous populations of lake trout where *Mysis* is absent. In these instances, estimates of potential yield should be reduced accordingly.

Anthropogenic stressors

Evans et al. (1991*b*) reviewed the impact of human activities on lake trout populations, and examined the manner in which lake trout responded to stress. They found that the response varied with the type of stress, but in general, a reduction in the lake trout's scope for activity was evident, ultimately leading to a decrease in population fitness and an increased risk of mortality (Priede 1977). Lake trout populations in such condition would be increasingly susceptible to catastrophic collapse resulting from a reduction in their numbers through exploitation.

In addition to exploitation pressure, Evans et al. (1991*b*) categorized the major stressors as species introductions and invasions, habitat and watershed modifications, and pollutants. Introduced or invading species frequently demonstrate an initial explosive growth in their population followed by a pe-

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riod of attenuation, resulting in a lengthy period of community instability. It is expected that invading species would have the greatest impact in small lakes with low fish diversity, as the bioenergetics of these systems could be substantially altered. Certain species have been documented to have significant effects on lake trout production, including rainbow smelt (*Osmerus mordax*), lake herring (*Coregonus artedii*), lake whitefish (*C. clupeaformis*), burbot, and walleye (*Stizostedion vitreum*) (Evans and Loftus 1987; Goddard et al. 1987; Carl et al. 1990; Matuszek et al. 1990). I have discussed earlier how *Mysis relicta* may affect the growth and yield of planktivorous lake trout. Other invertebrate invaders, such as zebra and quagga mussels (*Dreissena* sp.) may indirectly impact fish production by altering phytoplankton dynamics (Leach 1993; Nicholls and Hopkins 1993).

Habitat loss and watershed modifications may reduce the reproductive success and early survival of lake trout. Evans et al. (1991*b*) identified shoreline modification, substrate extraction, disposal of dredged materials, and water level fluctuations as having the greatest impact on habitat loss. The primary watershed effects are silt and nutrient loading caused by logging, agriculture, construction of roads and dams, and forest fires. Any of these occurrences can affect spawning substrate and early life habitat; for example, a water drawdown of as little as 0.3 m following lake trout spawning may result in a very high loss of eggs (DeRoche 1969). Once again, small lakes would be at greater risk because of the limited availability of these sites, and the fact that less wave energy is available to cleanse impacted areas.

Pollutants that may affect lake trout populations include domestic and industrial effluents, along with airborne toxicants. Acid deposition, for example, may cause successive recruitment failure through early life mortality (Beggs and Gunn 1986). Sewage effluent and septic fields contribute to an increase in nutrient loading, which results in a greater loss of hypolimnetic dissolved oxygen during summer. This may lead to increased juvenile mortality resulting from a higher vulnerability to cannibalism caused by concentrating the adults and small fish within a relatively restricted volume (Evans et al. 1991*a*). It is also possible that the corresponding reduction in water transparency may affect the efficiency of prey capture for sight feeders such as lake trout. Increased nutrient loading can promote algae growth in littoral areas, rendering the substrate unsuitable for spawning. This situation may persist following a lengthy rehabilitation period. Although nutrient concentrations have been reduced to the point where the eastern basin of Lake Erie is now experiencing near ultra-oligotrophic conditions at mid-lake (5.0 $mg \cdot L^{-1}$ total phosphorus), the nearshore regions continue to be degraded through continued high rates of *Cladophora* production (P.A. Ryan, Ontario Ministry of Natural Resources, Port Dover, Ont., personal communication).

Summary

Both fisheries managers and resource planners require tools through which a realistic assessment of potential fish production can be made on a lake by lake basis. This expectation should reflect the carrying capacity for the species indigenous to each lake, as modified by the factors that increase or constrain production. In this paper, a strategy is described through which these expectations and constraints can be logically assessed for lake trout populations (Fig. 1).

If a lake is to support a self-sustaining population of lake trout, it must be suitable with respect to the primary environmental determinants that control or limit the species (Fry 1947; Ryder and Kerr 1989). This can be established through application of the oxygen depletion models of Ryan and Marshall (1994), as demonstrated in Fig. 2. Lakes that experience a deficiency along one of the environmental axes would be unsuitable or marginal for lake trout in their current state. Unless conditions were improved, their future would be uncertain with regard to supporting a naturally reproducing stock of lake trout, let alone a sustainable fishery.

The next step is to determine whether other essential physical elements are in place for lake trout. Lake trout have very specific spawning and nursery requirements, and these sites can be readily degraded. If this critical habitat is in short supply, reproductive success and early age survival could be greatly diminished, and a fishery for naturally produced fish could not be expected.

If both environmental attributes and physical habitat are sufficient for lake trout, total community yield should be estimated to establish an upper bound to lake trout yield. A more precise estimate of potential lake trout harvest may then be made through application of the THV or lake area model (Figs. 3 and 4).

This estimate is preliminary only, as there are numerous lake-specific effects that may contribute to a lower observed yield. Lake size is a primary consideration, as species biodiversity can vary substantially in small lakes, especially those of surface area less than 1000 ha. Such lakes are exceedingly important, as they comprise more than 80% of Ontario's 2000+ lake trout waters (Martin and Olver 1976). If the fish community is simple, with a planktivorous lake trout population, a yield equivalent to the THV or lake area model might be expected; if not, resources must be partitioned among more species, and yield expectations for lake trout in these small lakes should be downgraded.

Human activities within the lake's catchment must also be assessed, as there are a number of potential stressors, besides fishing, that could contribute to a reduction in lake trout yield from the model prediction. As a general rule, small lakes would likely be more vulnerable to these cultural impacts and their lake trout populations would be more at risk of depletion and even extirpation triggered by the additional stress of exploitation. A cautious approach to yield estimation is advised when these conditions are encountered.

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Growth and development of North American stream habitat management for fish

Ray J. White

Abstract: Managing stream habitat for fish involves protection and ecological restoration, primarily to counter human-generated damage. Stream habitat work by public agencies, begun in Michigan trout creeks in 1927, is half as old as the continent's hatchery-based fishery management. It grew and changed, though many sound initial ideas remain in use. The field's geographic center shifted westward since about 1970. Early work concentrated on building wood and stone structures to repair in-channel damage from logging, soil cultivation, and grazing. Managers often used overly artificial methods unsuited to ecological needs, but cognizance of natural stream features and processes has increased, as has awareness of needs to deal more directly with harmful human influences. Forestry practices, soil tillage, and grazing persist as major problems, and other disturbances such as roads, pipelines, channelization, gravel mining, other mining, damming, water withdrawal, and urbanization receive increased attention. Emphasis remains on trout streams, but salmon habitat work has expanded, and habitat for warmwater fishes may be receiving increased attention. Growing emphasis on wild fish and on biotic integrity of ecosystems is an aquatic resource management trend, of which stream habitat management can be a beneficial part.

Résumé : La conservation de l'habitat des cours d'eau passe par la protection et par la restauration écologique, qui ont pour principal objet la réparation des dégâts causés par l'homme. Les travaux de conservation de l'habitat des cours d'eau réalisés par des organismes publics ont commencé dans les ruisseaux de truites du Michigan en 1927 et ils remontent à deux fois moins loin dans le temps que la gestion des pêches fondée sur les écloseries sur le continent. Ils ont été amplifiés et modifiés depuis ce temps, mais bon nombre des bonnes idées initiales ont été conservées. Leur centre géographique s'est déplacé vers l'ouest à partir des années 70. Les premiers travaux consistaient surtout à ériger des structures de bois et de pierre pour réparer les dégâts résultant de l'exploitation forestière, de l'épandage des boues et du broutage. Les responsables ont souvent employé des méthodes trop artificielles qui ne répondaient pas aux besoins écologiques; cependant, aujourd'hui, nous connaissons mieux les caractéristiques des cours d'eau et les processus qui s'y déroulent et nous reconnaissons la nécessité d'une action plus directe en ce qui concerne les interventions humaines nuisibles. Les pratiques de foresterie, le travail des sols et le broutage demeurent des problèmes importants et on se préoccupe de plus en plus d'autres perturbations comme les routes, les pipelines, les travaux de canalisation, l'extraction du gravier, d'autres types de travaux miniers, la construction de digues, le retrait des eaux et l'urbanisation. Bien qu'on s'intéresse surtout aux ruisseaux de truites, les travaux sur l'habitat du saumon ont augmenté et l'habitat des poissons des eaux tempérées pourrait recevoir une plus grande attention. Le poisson sauvage et l'intégrité biotique des écosystèmes prennent de plus en plus d'importance dans la gestion des ressources aquatiques, qui peut bénéficier de la conservation de l'habitat des cours d'eau.
[Traduit par la Rédaction]

Introduction

Until about 70 yr ago, almost all effort to improve stream habitat for fish was done privately by anglers in the British Isles and eastern North America. Stream habitat work of government agencies, which now prevails, probably dates from Michigan experiments in 1927. Agency programs took hold in the 1930s, spread widely after 1950, and have increased much since about 1970. This history is recent compared with over 130 yr of hatchery-based fishery management by agencies on this continent.

Stream habitat management has concentrated on cold-water sport fishes (though warmwater work dates from 1941; Lyons and Courtney 1990) and on small streams and their riparian zones rather than on large rivers and watershed-scale projects. Some reasons are that fish in most U.S. and Canadian streams are reserved for sport rather than commercial fishing, trout and their waters are highly prized, and small streams are more vulnerable to harm and more susceptible of manipulation than large ones. Anadromous salmonid habitat work recently expanded, especially in Pacific drainages. Effort has long been exerted on rivers of both coasts to contend with problems caused by dams and reservoirs; the adverse effects of migration blockage and of impoundment on salmon, sturgeon, shad, and other fishes are basically habitat problems but usually not labeled as such. Habitat management for anadromous salmonids also recently extended into estuaries. Broader watershed work, recognized as important for streams, is complicated by competing land uses and ownership problems and remains poorly developed.

As in fishery management in general, partially conflicting outlooks, motives, and objectives often confuse the focus of stream habitat work. These include (1) an agrarian ideology emphasizing technology and oriented toward producing com-

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modities (Bottom, in press), importantly fish for food and to support economic interests associated with sport angling; (2) an aesthetic and recreational value system associated with high regard for nature; and (3) a science of the ecology and genetics of natural systems. The first can result in overengineered channels, especially when combined with efforts to protect property against high water. It tends to be at odds with the latter two, which can easily complement each other.

In most fishery management, the agrarian ideology has predominated, strongly affected by industrial outlooks (see Lichatowitch 1992 on the contrast of industrial and natural economies). The fisher's objective has been to maximize catch, and the fishery manager's objective has been to ensure a supply of fish. Commercial fishers, applying an improving technology, generally succeeded in maximizing catch relative to existing fish stocks. But, given ecological, economic, social, and political complexities, managers generally failed to replace the catch and conserve wild fish stocks because they allowed overharvest and neglected to protect and restore habitat (Nehlsen et al. 1991; Alverson and Larkin 1994). Quests for quick gain overrode needs for sustaining quality of life and ecosystem health, the main focus being on "production" (harvest) of fish as a commodity. Sustained production, usually conceived as "maximum sustainable yield," was seldom achieved (Larkin 1977). Potential yield of noncommodity values was often overlooked or downplayed.

The sport fishery managers' objectives are more complex. They range from optimizing catch (and profit in commercial aspects, e.g., guides, tackle shops, motels, boat businesses) to accommodating subtle appreciations of resource users, such as those from making tackle, having a pleasant environment, and learning about streams, lakes, seas, and aquatic life. This calls for protecting habitat and sensitively restoring it where necessary and in keeping with human values.

Confusion between agricultural and ecological objectives and approaches was undoubtedly less a problem in stream habitat work than in the longer histories of fish stocking and harvest management. Recent advances in ecological understanding of streams and in "ecosystemic" approaches to habitat protection and restoration may dispel much of the confusion and light the way to more farsighted policies and actions.

For analytical purposes, we can assume that temporal and spatial patterns of stream (bitatÿÿÿfolloalpatbjectmatterinpublications. Therefore besides citing articles and presenting personal observations, I try to trace what happened before 1988 via statistics about the literature, using a major bibliographic source (Duff and Banks 1988); the authors state that it "primarily references structural and nonstructural stream habitat improvement" but includes some articles on "economic, political, and sociological pressures," categorized under "environmental planning." Therefore, the bibliograpy's emphasis and that of my paper is weighted toward technological aspects. Less attention is given the field's underlying philosophies, purposes, and science (e.g., habitat ecology of stream fishes), or its legislation, institutional arrangements and policies, funding, and relationships to other forms of resource management (forestry, mineral extraction, agriculture, etc.). Also, little is said about the history of the field's biological, economic, and social effectiveness, nor about the trend of anthropogenic stream habitat destruction that created the need for habitat management in the first place.

Methods

From the indexed bibliography on stream habitat improvement by Duff and Banks (1988), the most comprehensive compilation of the sort, having 1367 entries, I built a spreadsheet data base. The bibliography updated previous versions (Duff and Wydowski 1982; Duff and Gnehm 1986); author Duff contributed items acquired during his activity in the subject field, and Banks and a student team collected articles from journals and other library sources (D.A. Duff, U.S. Forest Service, Salt Lake City, Utah, personal communication). Besides professional papers and official reports, the bibliography listed intra-agency reports, theses, newsletter excerpts, and a few magazine or newspaper articles. For each item, my data base contained the following information to the extent shown in the bibliography, evident in the title, or otherwise known to me: (1) article identification number (in the bibliography); (2) year of issue; (3) subject country (not necessarily source country); (4) subject state or province, if in North America (not necessarily the source state or province); (5) subject region in North America; (6) source institution (or journal) of the article; (7) whether (6) was classed as a state, provincial, or federal agency (others not classified); (8) type of publication (professional journal, agency report, thesis, etc.); (9) topical (subject matter) area (Table 1); and (10) whether the article was printed or in audiovisual form.

In the data base, I omitted authors' names, titles of articles, and volume and page numbers.

Determining the pertinent topics in articles involved considerable inaccuracy. Topic identification was mainly from titles; neither I nor apparently the bibliography compilers had time to read or even see all the articles. Also, many topics were overlapping or otherwise indistinctly identifiable, e.g., if a stream habitat component was mentioned in a title, it was not always apparent whether management of it was also involved. Thus, loose interpretation was often unavoidable. Resultant flaws in the data set require that characteristics and trends indicated in analyses of topics be regarded as general. Lack of a specific topic descriptor for fishing is a drawback of the data set and analysis because responses to habitat management in terms of sport and commercial catch and other fishery attributes are important.

Under these limitations, I tallied the articles' pertinent subjects according to 58 main descriptors ("key words") and three modifying descriptors: guideline, technique, and general (Table 1). Duff and Banks (1988) had classified the articles according to the three modifiers and 17 main descriptors, of which I adopted all except "obstruction removal" because sometimes it was not pertinent or was ambiguous in relation to habitat, and because some (perhaps most) programs to remove such obstructions as log (and other wood debris) jams have harmed more than helped fish. As I entered articles into the data base, I developed and added 45 topic descriptors (Table 1; nonbold numbered items) that suggested themselves from titles, or that I knew from having examined articles. These pertained to streams, stream habitat, stream fauna, habitat assessment, habitat management, other human activities affecting stream habitat, evaluation of habitat projects, etc. (Table 1; other unused but logical topic descriptors are shown in brackets). Most of the bibliography's descriptors had been defined in terms of activities in or effects from "stream habitat improvement," yet many of them dealt primarily with other aspects, e.g., stream characteristics or methods for measuring them, so I adjusted these previous determinations. I also added descriptors found in or inferred from titles indicating that articles should be omitted from the present analysis. These included bibliographies; articles on marine, estuarine, and lacustrine topics; and duplications of listed articles.

Where possible, I corrected such errors in the bibliography as duplicate listings, omissions of issue year, misclassifications of sub-

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Table 1. Occurrence frequency of subjects related to stream habitat management in (or inferred from titles of) articles in the Duff and Banks (1988) bibliography.

		Occurence frequency				
		Definite mention				
				% since[a]		
General category	Subject	No. of articles	(% of N)	1970	1980	Unsure
A. Stream habitat components /types	1. In-channel structure (often called "cover")	328	(27.2)	69	43	24
	2. Riparian vegetation/processes	309	(25.7)	87	43	22
	3. **Streamflow discharge** (also control of)	244	(20.3)	85	43	18
	4. Spawning habitat	80	(6.6)	78	58	13
	5. Channel morphology	39	(3.2)	69	38	37
	6. Large woody debris (LWD)	24	(2.0)	79	71	6
	7. Bed material	17	(1.4)	88	59	6
	8. Aquatic vegetation	13	(1.1)	92	23	5
	9. Winter habitat	5	(0.4)	100	80	3
	[*Channel hydraulics*]					
	[*Fine woody debris (FWD)*]					
	[***Chemical water quality***][b]	[117]	(9.7)	[75]	[43]	[18]
	[***Thermal water quality***][b]	[49]	(4.1)	[75]	[29]	[9]
	[*Thermal refuge*]					
	Subtotal or mean	1059[c]		80	45	
B. Stream fauna	10. **Invertebrates**	67	(5.6)	88	39	4
	11. **Coldwater fish** (salmonids)	444	(36.9)	73	46	Many
	12. **Warmwater fish**	63	(5.2)	81	48	2
	13. Coolwater fish (pike, percids, smallmouth bass)	11	(0.9)	100	64	0
	14. Beaver	9	(0.7)	67	56	0
	[*Other vertebrates, e.g., muskrat, mink, otter, birds, reptiles, amphibians*]					
	Subtotal or mean	594[c]		76	46	
C. Human activities that degrade habitat, and consequences	15. **Sediment runoff, deposition** (not control thereof)	190	(15.8)	74	36	15
	16. Livestock grazing	120	(10.0)	92	56	10
	17. Timber harvest, forestry	69	(5.7)	86	43	7
	18. Channelization, other dredging	63	(5.2)	90	24	25
	19. Removal of large woody debris ("snagging")	37	(3.1)	78	46	15
	20. Roads, highways (including culverts, bridges)	35	(2.9)	94	35	1
	21. Damming, impoundment-related	23	(1.9)	95	50	6
	22. Other mining (mineral, oil, gas extraction)	19	(1.6)	68	47	1
	23. Water withdrawal for crop irrigation	10	(0.8)	50	10	18
	24. Urban, industrial development	9	(0.7)	78	33	0
	25. Gravel mining	8	(0.7)	100	75	1
	26. Cultivation agriculture	3	(0.2)	67	33	22
	[*Off-road vehicle use in streams, on stream banks*]					
	[*Pipelines*]					
	[*Streambank destabilization*]					
	[*Removal of streambank vegetation*][d]					
	[*Removal of aquatic vegetation*][d]					
	[*Discharge or runoff of chemical wastes*]					
	[*Discharge of heated water*]					
	[*Increased overland runoff of water*]					
	[*Water withdrawal for urban/industrial supply*]					
	Subtotal or mean	586[c]		83	41	
D. Habitat managements	27. Streambank stabilization	237	(19.7)	82	44	18
	28. **In-channel structures** (item 1 + technique or guideline)	163	(13.5)	68	46	20
	29. **Spawning habitat improvement** (item 4 + technique or guideline)	122	(10.1)	80	47	15

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Table 1. *concluded.*

General category	Subject	Occurence frequency: Definite mention: No. of articles	(% of N)	% since[a]: 1970	1980	Unsure
	30. **Riparian vegetation management** (item 2 + technique or guideline)	107	(8.6)	91	51	18
	31. **Livestock exclosure** (streambank, riparian fencing)	72	(6.0)	94	56	2
	32. **Fishways** (for small streams)	24	(2.0)	96	70	4
	33. Watershed programs	24	(2.0)	75	17	3
	34. Stream fertilization	8	(0.7)	75	63	0
	35. Channel relocation (restoring meanders, etc.)	2	(0.2)	50	0	1
	36. Ecosystem management	2	(0.2)	100	50	2
	[Obstruction removal][e]					
	[*Streamflow discharge control* (see item 3)]					
	[*Beaver management (introduction or removal)*]					
	Subtotal or mean	758[c]		81	47	
E. Habitat assessment	37. Biological survey	13	(1.1)	83	33	20
	38. Habitat assessment	47	(3.9)	98	57	29
	39. Assessment method (item 38 + technique or guideline)	8	(0.7)	100	50	0
	40. In-stream flow needs studies	17	(1.4)	94	35	6
	Subtotal or mean	85[c]		95	35	
F. Evaluation of habitat management	41. Evaluation results	123	(10.2)	70	43	44
	42. Evaluation methods	10	(0.8)	90	80	3
	Subtotal or mean	133[c]		71	45	
G. Other biological aspects	43. **Fish ecology or behavior**	194	(16.1)	82	51	7
	44. Habitat use by fish	55	(4.6)	84	55	11
	45. Fish passage	37	(3.1)	82	47	10
	46. Community ecology	9	(0.7)	100	56	11
	47. Ecosystem effects	8	(0.7)	100	0	14
	48. Riparian ecosystems	6	(0.5)	100	33	22
	49. Ecosystem theory	2	(0.2)	100	50	1
	Subtotal or mean	311[c]		84	49	
H. Other physical aspects	50. Hydrology	33	(2.7)	67	24	13
	[***Fish screens***][b]	[4]	(0.3)	[100]	[100]	[0]
	Subtotal or mean	33		67	24	
I. Other human aspects	51. **Environmental planning**	139	(11.5)	71	59	3
	52. Economic aspects	15	(1.2)	87	27	0
	53. Land use (general)	12	(1.0)	83	8	2
	54. Recreation (including angling)	12	(1.0)	83	25	3
	55. Human social impacts	7	(0.6)	100	71	4
	56. Political aspects	3	(0.2)	100	100	2
	57. Aesthetics	2	(0.2)	100	0	2
	58. Legal aspects	2	(0.2)	50	0	2
	Subtotal or mean	192[c]		75	52	
J. Modifiers	59. Techniques	277	(23.0)	71	43	34
	60. **General**	264	(21.9)	63	42	4
	61. **Guidelines**	257	(21.3)	73	35	5
	Subtotal or mean	798[c]		69	40	

Note: Subjects (key words) designated by Duff and Banks (1988) are shown in bold. Other pertinent subjects not found or not analyzed (except in some cases as ancillary subjects) are italicized in brackets. ($N = 1204$; see Methods).

[a]Adjusted for undated entries in the bibliography (Duff and Banks 1988).

[b]A major subject in the bibliography, but articles dealing with it were detected for the present paper, except when ancillary to other subjects.

[c]Overlapping mention between items above requires this to be regarded as an index of frequency, not number of articles within the general category.

[d]Other than for fish habitat manipulation.

[e]A major subject in the bibliography, but not used in the present paper because it was in some titles ambiguous in relation to habitat, also often not in keeping with modern concepts of habitat restoration.

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ject, and insufficient subject descriptions. Duplication errors often resulted from misspelt author names. I also discarded symposium proceedings if component papers occurred separately in the bibliography. As mentioned above, considerable error had apparently happened (and I undoubtedly introduced more) by inferring from some titles subject matter that did not occur in articles, and I found and corrected some of this via familiarity with articles or by checking the text of others.

Besides removing the 23 bibliographies listed in the source bibliography, I deleted 10 articles that seemed not to pertain to habitat, 2 that dealt only with marine or estuarine environments, and 14 that covered lakes or ponds only. To focus analysis more narrowly on the classical physical and vegetational aspects of natural stream habitat and its restoration, I also deleted 25 "fishway" articles that seemed relevant only to massive installations associated with large dams (matters of culverts and other road-crossing passage were retained), 11 dealing narrowly with fish screens, and 40 that were mainly water quality description. I kept the few relating directly to chemical techniques, e.g., stream fertilization or liming to neutralize acidity. The resultant data base contained 1204 articles, of which 1186 included year of issuance. Because the bibliography was issued in July 1988, many of that year's articles could not be included; therefore, I excluded 1988 data from various time analyses.

Results and discussion

Limitations of the data source

When analyzing and interpreting the material in Duff and Banks (1988), topical, temporal, and geographical biases of the data should be recognized. The bibliography's intended topic was improvement of stream habitat for fish, which implies narrower scope than habitat management. Improvement has often meant primarily manipulation of in-channel structure. Therefore, less coverage of other aspects of stream habitat and its management would be expected, and this was indeed so. More attention in future bibliographies to broader stream habitat management and the science on which it should be based should promote better habitat work. Coverage of articles on warmwater stream habitat was sparse; Duff and Banks (1988) included only 13 of the 32 pre–1988 sources that Lyons and Courtney (1990) referenced on this subject.

Temporal bias can be expected from the lesser likelihood of articles being found if they were so old as to be rare or obscure or if they were relatively recent and, therefore, had less time to come to compilers' attention.

Because the bibliograpy's compilers were in Utah and associated with the U.S. Forest Service, there was undoubtedly under-representation of articles not from Utah, adjacent states, and federal agencies in that region of much U.S. federal land ownership. Eastern states lie distant from Utah and contain far less federal land. Missing were some key papers from the U.S. Pacific coast on salmonid habitat use (Cederholm et al. 1981; Cederholm and Scarlett 1981; Bisson et al. 1982; Scarlett and Cederholm 1984; Peterson and Reid 1984) and on forestry effects (Bisson et al. 1987; Sullivan et al. 1987).

Coverage of Canadian sources was especially limited. Absent, for example, were proceedings of the Carnation Creek workshops: 19 papers in Hartman (1982) and 16 in Chamberlin (1987). These papers helped develop the habitat management embodied in revamped B.C. coastal fishery–forestry guidelines. Other significant Canadian papers on relationships of salmonids with stream habitat, its management, and other habitat-affecting human activities were lacking, particularly on logging (e.g., Narver 1972; Scrivener and Brownlee 1981; Toews and Moore 1982; Tschaplinski and Hartman 1983; Hartman et al. 1984, 1987; Scrivener and Andersen 1984; Brown 1985; Hartman and Scrivener 1986; Poulin 1986; Hartman and Brown 1987). Not included on instream flow matters were Shirvell (1986) and Scott and Shirvell (1987), as was Burt and Mundie's (1986) extensive review of 81 case histories on effects of regulated stream flow on salmonid populations.

Topic frequency

Stream habitat components composed the general substantive (nonmodifier) category receiving most mention in articles (Table 1, category A), as would be expected in a bibliography on this subject. Also as expected, stream habitat managements composed the category of second most frequent mention (Table 1, category D). That only about half of the articles dealt with management (the 758 overlapping key word occurrences may represent less than half of the 1204 articles) indicates a certain breadth of material having basic and supplementary value in considering the main subject (but note the comments above and elsewhere on limitations in that regard). Anthropogenic harm to stream habitat (category C) was also heavily represented (586 occurrences), as was mention of other, often basic biological aspects (category G, 312 occurrences).

Habitat components

The components most often dealt with were in-channel structure (27% of articles) and riparian vegetation (26%), the latter playing a major role in channel structure (Table 1). These emphases are consistent with the field's traditional focus on structural habitat. Streamflow discharge followed at 20%. Spawning habitat and channel morphology were far less often covered. Large woody debris, aquatic vegetation, and winter habitat were represented by few articles. Chemical water quality was an ancillary subject in about 10% of articles and thermal water quality in 4% (recall that I deleted articles featuring these two topics as the major subjects).

Fauna

The animals most mentioned or implied in titles were cold-water fishes (37% of articles). Salmonids were the object in further articles that did not specify them in the titles. Warmwater fishes were designated in 5% of titles, and cool-water fishes in 1%. Invertebrates were involved in 6% of articles and beaver in less than 1%. No other wild fauna occurred in the titles.

Anthropogenic harm

The largest class of habitat-harming human activities (or physical consequences thereof) in the articles was sediment runoff–deposition (16% of all articles), followed by livestock grazing, timber harvest – forestry, and channelization, removal of woody debris, and road–highway matters. Strong interrelatedness of topics in this group is obvious.

Habitat managements

Most mentioned was streambank stabilization (20% of all articles), followed by in-channel structures, improvement of spawning habitat, management of riparian vegetation, and livestock exclosure. Streambank stabilization may have been

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the most mentioned aspect in management-related articles because it is integral to in-channel structural work in many habitat projects of other sorts, and because protection of "real estate" (a nonfishery aspect) against encroachment by streambank erosion is a concern for many people.

Stream habitat assessment

This category (category E, 85 occurrences), sometimes termed "habitat evaluation," is the quantitative and qualitative analysis of stream habitat for fish. It is not to be confused with evaluation of habitat management but often is involved in analyzing needs for habitat management. The category contained a few articles on general biological surveys but was composed mainly of those on assessing fish habitat specifically. The topic of instream flow needs seldom occurred; apparently the compilers had not dug deeply into the large literature on that subject. The Orsborn and Allman (1976) proceedings on a major instream flow needs symposium was listed but not the many pertinent papers in it. Also missing were papers from the series of symposia on ecology of regulated rivers (Ward and Stanford 1979; Craig and Kemper 1987).

Evaluation of habitat management

This group (category F, 133 occurrences) included primarily reports of results, although reviewing the content of articles reveals that some, especially early ones, were very general or covered only physical durability of structural work, not responses in terms of fish abundance, fish behavior, or fishing. Ten articles dealt mainly with evaluation methods.

Other biological aspects

Pertinent studies on fish ecology and (or) behavior (involved in 16% of articles) accounted for the vast majority of occurrences in this catchall category. Habitat use by fish, an important, closely related topic, seldom occurred. Fish passage was involved in 3% of articles (after articles on some kinds of fishways were deleted). Topics involving community ecology and ecosystem ramifications were lightly represented; the compilers may have considered such matters as beyond the bibliography's scope. The literature (certainly that before 1988) probably contains little about stream habitat management's effects at ecosystem or community levels.

Other human aspects

Human aspects other than habitat management and degradation were not abundant. Environmental planning, the most common topic in this category, seems so vague a concept as to be inconsequential, and none of the rest of the topics (economic, political, social, etc.) occurred in more than 1% of articles. Even recreational implications, including angling, were rare; omission of specific references to fishing in the choice of key words probably accounts for this (see Methods).

General time trends

North American stream habitat work was predated by that in the British Isles (Hubbs et al. 1932). There, Boccius (1848) described causes of fish depletion in writing on artificial propagation of fish. The British authors wrote mainly on angling. They concentrated stream management comments on trout stocking, removal of predatory northern pike (*Esox lucius*), and contending with poaching and said little about structural habitat beyond the cutting of aquatic plants that interfered with angling (Dick 1873; Halford 1903). North American stream habitat articles first appeared in the 1930s, influenced no doubt by the British work, by the beginnings of applied ecology, and by the turn of the century conservation and forestry movement. In the latter, Leopold (1933) attached importance to Theodore Roosevelt's 1909 idea of using science to further conservation, and he noted that American environmental control for wildlife began about the mid–1920s. Stream habitat work was not far behind.

Duff and Banks (1988) listed only five articles predating 1931: Boccius (1848), two other British books (Armistead 1908; Platts 1927), the first North American listing (Paul and Barnes 1913) which was a Utah newspaper article, and a report on a general biological survey (Forbes 1928), which may have had little bearing on habitat management. A listed paper by Brown (1922) on "adjustment of environment vs. stocking" may be the earliest article in the *Transactions of the American Fisheries Society* (52 yr after the journal's start) on habitat improvement, but it pertains to lakes, not streams. Pertinent pre–1931 publications not in Duff and Banks (1988) are referenced in Hubbs et al. (1932): two British books (Malloch 1910; Mottram 1928), a German book (Walter 1912), and one on American trout stream problems and management (Ingraham 1926).

Publication on government stream habitat programs probably began with Tarzwell's (1931) description of Michigan's work in a paper presented at the American Fisheries Society's 1930 annual meeting. The chemist-angler, Hewitt (1931), wrote a contemporary book on his private habitat work. Thereafter, except for interruption by World War II, North American literature on the subject appeared annually and generally grew (Table 2, Fig. 1).

The first comprehensive publication on the subject was a University of Michigan bulletin by Hubbs et al. (1932), which incorporated a history of stream improvement. They reported that Michigan's first official stream habitat work was undertaken in 1927 by Dr. Jan Metzelaar, "Fisheries Expert for the State Department of Conservation." They explained that until their experimentation began about 1930 (apparently for the Michigan Department of Conservation), American stream improvement for fish had been done largely on private estates and clubs in New York and Michigan, as in Britain.

The Hubbs et al. (1932) manual and its annotated bibliography indicated the era's confusion about the scope of stream habitat management. The bulletin concentrated on how to build instream structures and included water quantity and quality, spawning habitat, aquatic vegetation, streamside vegetation, and beaver problems. However, it covered much else that today is considered outside the realm of habitat, namely, control of predators and competitors, how to increase trout food abundance, establishing no-fishing refuges to prevent overharvest, and reducing trout populations to improve body growth. The booklet even dealt with aspects of hatchery-trout stocking.

The 1930s' publication increase (Fig. 1) corresponded with U.S. Government make-work programs of the Economic Depression, giving technical guidance and reporting on progress. The number of articles peaked in 1935, probably preceding most of that era's habitat work, which may have climaxed

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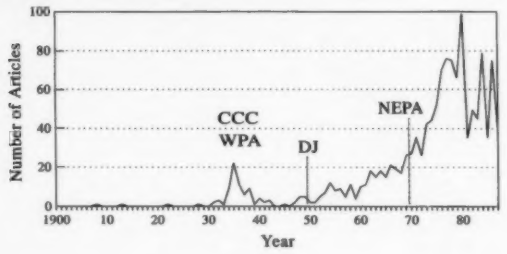
Table 2. Decadal frequency of dated, pertinent articles in Duff and Banks (1988).

Period	No. of articles	Per cent of total
Pre-1930	4	0.3
1930–1939	63	5.3
1940–1949	21	1.7
1950–1959	58	4.9
1960–1969	153	12.9
Pre-1970*subtotal	299	25.2
1970–1979	451	38.0
1980–1988**	436	36.8
1970–1988 subtotal	887	74.8
Total	1186	100.0

*The 1970 break point adopted because that year marked Earth Day and NEPA.

**The bibliography was issued in July 1988

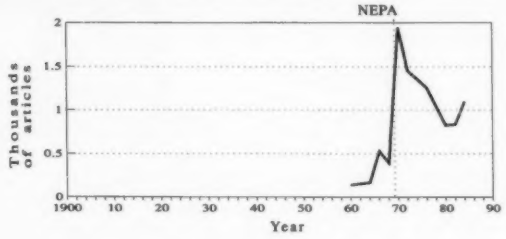
Fig. 1. Time frequency of stream-habitat-related articles in Duff and Banks (1988). N = 1306 (61 other entries in the bibliography were duplicates, undated, or non-habitat). CCC (Civilian Conservation Corps) and WPA (Works Progress Administration) indicate the period of the job-creation programs of the U.S. government during the Great Economic Depression; DJ = the U.S. Dingle-Johnson Act of 1950, levying a tax on fishing tackle sales to support fishery management and research; NEPA = U.S. National Environmental Protection Act.



about 1941, just before U.S. entry into World War II. Of 1935's 22 articles, 18 were from the U.S. government (Bureau of Fisheries and Forest Service), and federal personnel undoubtedly authored some of the remainder, which appeared in other outlets.

The increasing numbers of stream habitat articles after World War II (Fig. 1) may represent an exponential growth process but may also reflect influences of several major events. Although annual numbers rose in the late 1940s, the main postwar increase began in the 1950s, perhaps lagging behind growth of the habitat work itself. Funding from the Dingell–Johnson Act of 1950 undoubtedly spurred progress, and publication increased at a moderate rate during the 1950s and 1960s, reaching about 20 articles/yr in the late 1960s. The late–1960s surge in public environmental awareness (Fig. 2), culminating in the National Environmental Policy Act (NEPA) of 1969 and Earth Day (22 April 1970) was followed by rapid growth in publication, which peaked at almost 100 articles in 1980 (Fig. 1). Since then, annual output of pertinent articles has fluctuated greatly (35–79 articles/yr) around a lower mean of about 50. The spikes of 1980, 1984, and 1986

Fig. 2. Time frequency of New York Times articles on environmental topics as an index of American public interest in environmental issues. Data source: Wenk (1986).



coincide with years in which proceedings (Seehorn 1980; Hassler 1984; Miller et al. 1986) were issued for the informal North American stream habitat improvement workshops, held biennially since 1978.

The 1976–1980 peaking in annual number of articles and the reduction during the 1980s (Fig. 1) may represent a wave of stream habitat work that developed from the environmental fervor, which crescendoed in the early 1970s and markedly declined late in that decade (Fig. 2). Lack of time for articles to come to the bibliography compilers' attention may partly account for the apparent decrease in the 1980s, especially just before the bibliography date.

Stream habitat literature's attention to cool-water fishes, which was minor, all occurred after 1970, whereas 19% of articles involving warmwater fish and 27% of those involving cold-water fish appeared before 1970 (Table 1). Of papers involving cool-water fish, 64% occurred in 1980–1988. The comparable figures for warm- and cold-water fish were 48% and 46%, respectively.

Time trends of component topics

In the field's 1930s inaugural era, most articles focused on description of techniques, especially in-channel structural "devices." As is inevitable for a nascent field, the publications contained some fanciful ideas, later found ineffective or harmful. But generally the early authors were ecologically oriented, stream-savvy biologists, whose ideas and designs suited the kinds of waters with which they had experience, usually Midwest spring creeks of relatively stable flow and some steeper streams of the Rocky Mountains but not the exceedingly high-energy streams of the Pacific Coast. Many early methods stood the test of time and are still used in spring-dominated waters of the East, Midwest, and Rocky Mountains. The techniques often failed physically in West Coast mountain streams.

Usually the early biologists prefaced technique manuals by discussing trout habitat requirements and offered wise, fundamental advice. This may have offered the first agency stream habitat managers a sounder ecological footing than generally existed in other branches of fishery work then. Hubbs et al. (1932) covered roles, "practicality," history, planning of habitat work, and the trout's requirements before describing some 30 in-channel devices, management of streambank vegetation, and other measures. A derivative U.S. Bureau of Fisheries methods booklet "for the use of stream improvement workers" (Davis et al. 1935) discussed the purpose of habitat work and recommended using simple structures, adapting them to stream character, having the work guided by personnel who

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Fig. 3. Percent temporal occurrence during 1970-1988 of those topics which occurred >30 times in dated, stream-habitat-related articles in Duff and Banks (1988). Percent pre-1970 occurrence = 100 minus the 1970–1988 occurrence. *management; **anthropogenic harm.

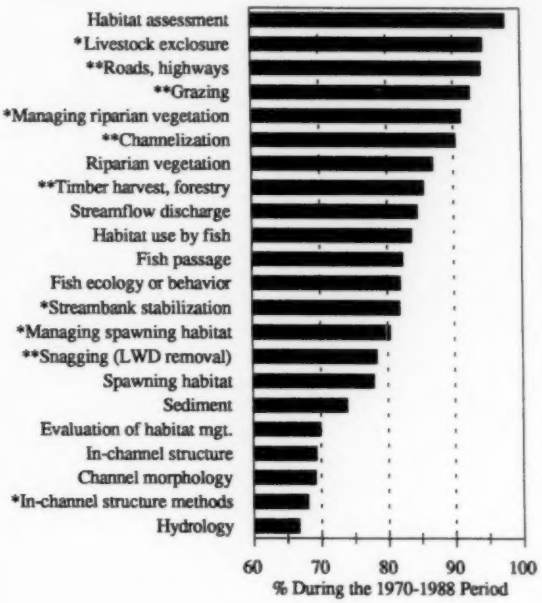
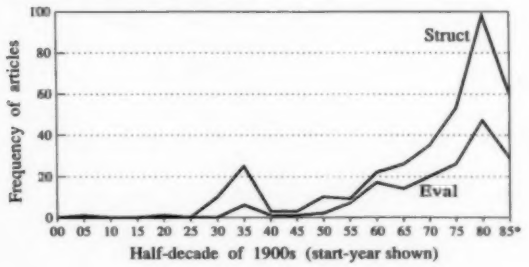


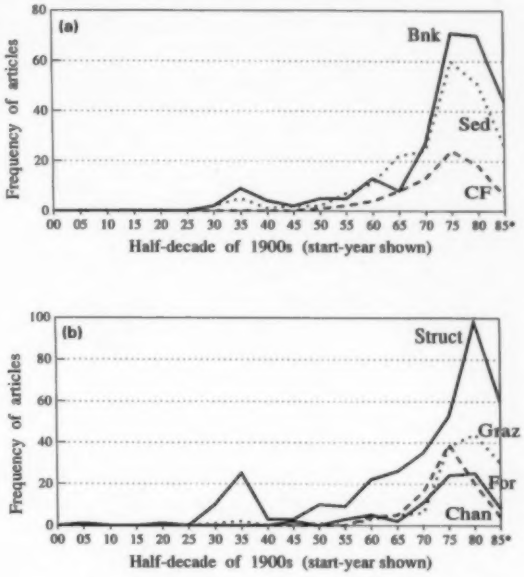
Fig. 4. Time frequency of articles dealing with in-channel structure, including management of structural habitat (Struct), and of articles reporting evaluations of stream habitat management (Eval). *Data ended in 1988.



understand fish and streams, making thorough preliminary studies of the stream as a whole, and exercising moderation. That advice still applies, and always will. Often it has been overlooked and lost to institutional memory in agencies, occasionally being independently redeveloped. The stream habitat wisdom gained in those early years and since should be acknowledged and emphatically reiterated in new publications, so that it can be better known and used.

Early emphases of the field can be inferred from statistics on proportions of articles occurring before and after some intermediate moment, e.g., the environmental movement's crucial year, 1970 (Table 1, column 5; Figs. 1 and 3). Among topics occurring in 20 or more articles, "general" information on stream habitat or its management had the highest pre–1970

Fig. 5. Time frequency of stream-habitat-related articles in Duff and Banks (1988) dealing with (a) sediment (Sed), streambank stability (Bnk), and channel form (CF), and (b) livestock grazing (Graz), forestry-related topics (For), channelization (Chan), and in-channel structure (Struct). *Data ended in 1988.


(a)
Bnk
Sed
CF
Frequency of articles
00 05 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85*
Half-decade of 1900s (start-year shown)
(b)
Struct
Graz
For
Chan
Frequency of articles
00 05 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85*
Half-decade of 1900s (start-year shown)

proportion of incidence (37%). This contrasts with the data base's overall 25% proportion of pre–1970 articles (Table 2). General publications were especially numerous in the 1930s. Other topics of high pre–1970 proportion (Fig. 3) were hydrology, in-channel structural methods, in-channel structure per se, and channel morphology; the latter three topics were almost synonymous and much intermingled.

Evaluation of habitat management had a slightly higher than average pre–1970 proportion of articles (Fig. 3), and the time pattern of evaluatory items closely shadowed that for in-channel structural habitat (Fig. 4). This may signify healthy self-examination within the profession but may also reflect pressure from agency administrators who were skeptical about habitat work, saw it as competition for hatchery programs, and opposed spending money on it (personal observation from agency service and from habitat-involved colleagues in many agencies). That the few articles specifically examining methods of evaluation are mostly recent (90% since 1970; Table 1) may indicate growth in evaluatory rigor.

Articles on sediment matters were of average temporal distribution (Fig. 3; mean proportions for all subjects: 25% pre–1970, 75% 1970–1988), having had attention from the field's start (Fig. 5*a*). The related subject, streambank stabilization, also well represented early on, was treated in a higher proportion of post–1970 articles than sediment (Figs. 3 and 5*a*). Both relate closely to channel morphology, which did not occur as a subject in stream-habitat literature until the 1950s (Fig. 5*a*) but had high pre–1970 proportion (Fig. 3).

Ascending most sharply after 1970 (Table 1) were stream habitat assessment (category E; 95%), attention to anthropogenic harm (category C; 84%), and consideration of ecology

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in relation to habitat work (category G, other biological aspects; 83%). The differences between the latter two and some other categories (habitat components, 80%; habitat managements, 81%) are small and probably nonsignificant; undoubtedly, these general categories overlapped much within articles.

Specific major topics (>30 articles; Fig. 3) showing recent rise in occurrence include habitat assessment studies, livestock exclosure, road or highway aspects, livestock grazing, management of riparian vegetation, channelization, riparian vegetation, forestry-related matters, streamflow discharge, and habitat use by fish. Large woody debris (LWD) and winter habitat matters also appeared very recently as subjects, and were still represented by few articles as of 1988 (Table 1).

Strong presence of certain topics among those having high recent proportion (Fig. 3) may indicate trends toward greater ecological awareness, managerial efficiency, and attention to fundamental causes of habitat degradation. Habitat assessment's high recent proportion may imply a rise in premanagement problem analysis. Almost half of the other more recent than average topics show attention to anthropogenic harm (roads, grazing, channelization, timber harvest, and LWD removal; Fig. 3), including livestock exclosure, which is a way of reducing such harm. Second to livestock exclosure in recent management emphasis was riparian vegetation management, which also connotes long-term objectives. These stand in contrast to traditional direct restructuring of streams, as encompassed by the topic, in-channel structure management, which had a relatively low proportion of its articles during 1970–1988 (Fig. 3), but its absolute numbers remained high (Figs. 4 and 5*b*). Articles on grazing, forestry, and channelization became frequent later than those on in-channel structure (Fig. 5*b*).

Geographical distribution

For the total period of coverage, the articles had four geographic concentrations (Table 3, Fig. 6): (1) Appalachia from New Hampshire and Vermont south to West Virginia; (2) the Great Lakes area of Wisconsin, Michigan, Ohio, and southern Ontario; (3) the Rocky Mountain area of Montana, Idaho, Wyoming, Utah, and Colorado; and (4) the Pacific Coast states of Oregon and California, plus British Columbia. Alaska is so vast that even its fair number of articles (21) could not qualify it for concentration status. The absence of Maine and Washington state from the areas of concentration is notable, given their important stream fisheries.

The region most often the subject of articles (Table 3) was the Pacific Coast (233). The sparsely populated Rocky Mountain region, however, had almost as many articles (206) and was highest in number of articles per capita and per unit area.

The most frequent subject jurisdictions were Oregon (75 articles), California (63), and Wyoming (62). Bunched between 38 and 24 articles were Utah, Wisconsin, British Columbia, Montana, Idaho, Michigan, and Colorado, in that order. The foregoing 10 jurisdictions probably include most of those that, at some time during 1931–1988, had the continent's most vigorous stream habitat programs. But the order and to some extent the composition of this group would probably change if correction were made for the aforementioned geographic biases of the data base, particularly the inadequate coverage of Canadian articles.

Wyoming had by far the most articles per capita, and other jurisdictions having low human populations and large salmonid stream resources also had high numbers of articles per capita, such as (in order) Alaska, Montana, Idaho, Utah, Oregon, and British Columbia (Table 3). For jurisdictions having ≥20 articles, Oregon had the most per unit land area, followed in order by Wisconsin, Wyoming, Michigan, Utah, California, Idaho, Colorado, Montana, British Columbia, and Alaska (Table 3).

The pre–1970 areas of article density were much different and more scattered (Fig. 7). They consisted of (1) New Hampshire (perhaps combined with Massachusetts and New York); (2) West Virginia; (3) Michigan and Wisconsin; (4) Montana; (5) California; and (6) perhaps New Mexico, the latter due to early federal writings. In most of the interior western states, the hiring of biologists and the practice of fishery management other than stocking and law enforcement began only about 1950 (Wiley 1994), whereas in Canada, some eastern states, and on the U.S. West Coast, fishery agencies had employed biologists since at least the 1920s.

The concentrations of 1970–1988 articles (Fig. 8) were in (1) a group composed of southern Ontario, New York, Pennsylvania, West Virginia, and Ohio; (2) Wisconsin; (3) the Rocky Mountain belt of Montana, Idaho, Wyoming, Utah, and Colorado; and (4) Oregon. During this period, the largest numbers of articles originated from Oregon and Wyoming, and 68% of articles applied to jurisdictions from the Great Plains westward; whereas, of the pre–1970 articles, only 53% were from that area. The westward shift of the field's geographic distribution since 1970 coincided with the expansion of biological staffs in western state fishery agencies, the broadening of U.S. Forest Service and Bureau of Land Management missions, and the hiring of many more fishery biologists in those federal agencies. Also evident was reduced stream habitat publication featuring the New England states, Michigan, and New Mexico. Filtering out the U.S. and Canadian federal publications to better indicate state and provincial agency and university effort (but not filtering federally authored papers from journals and non-federal symposia) changes the order among the highest three states to Wyoming (58), California (53), and Oregon (52); Wisconsin (32) moves up to fourth place, followed by British Columbia (30), Utah (28), Montana (27), and Colorado (26), Michigan (18), Idaho (17), and Ontario (17). Thus, reducing the federal component shifts the distribution eastward.

Post–1988 developments

Influence of wild fish policies

Managing for wild fish is a recent North American trend. The concept of wildness, with the naturalistic attitudes and policies it implies, is increasingly invoked in fishery work. Wild trout symposia have been held in Yellowstone National Park at 5-yr intervals since 1974, other conferences and publications on the subject abound, and some conservation groups are dedicated to wild salmonid resources, e.g., Trout Unlimited, Trout Unlimited Canada, Federated Fly Fishers, California Trout, Oregon Trout, and Washington Trout. Most agencies that deal with salmonids are adopting wild fish policies and programs (White et al. 1995*b*). For example, British Columbia has conservation of wild fish and maintenance of their habitat as its

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Table 3. Frequency of stream-habitat related articles in Duff and Banks (1988) in regions and political jurisdictions, showing also articles per capita human population and article density per land area. Human population data are from the U.S. 1970 and Canadian 1971 censuses, an approximation of the mean date of the articles.

Region	State or province	No. of articles	Population in 1970–1971	Area (km^2)	Population density (no./km^2)	Articles per million people	Articles per 10 000 km^2
Northeast	N.Y.	19	18 241 391	123 890	147.24	1.04	1.53
	Pa.	17	11 800 766	116 617	101.19	1.44	1.46
	Que.	9	6 027 800	1 356 800	4.44	1.49	0.07
	N.H.	5	737 681	23 395	31.53	6.78	2.14
	N.B.	4	634 600	73 437	8.64	6.30	0.54
	Vt.	4	444 732	24 020	18.52	8.99	1.67
	Mass.	4	5 689 170	20 287	280.43	0.70	1.97
	Maine	3	996 722	80 116	12.44	3.01	0.37
	Conn.	2	3 032 217	12 613	240.40	0.66	1.59
	N.J.	2	7 171 112	19 508	367.60	0.28	1.03
	R.I.	2	949 723	2725	348.56	2.11	7.34
	Del.	1	548 104	5136	106.72	1.82	1.95
	N.S.	1	789 000	55 491	14.22	1.27	0.18
	P.E.I.	0	111 600	5657	19.73	0.00	0.00
	Nfld.	0	522 100	404.519	1.29	0.00	0.00
	Northeast general	3					
	Northeast total	76	57 696 718	2 324 212	24.82	1.32	0.33
Southeast	W.Va.	17	1 744 237	62 378	27.96	9.75	2.73
	N.C.	6	5 064 411	127 084	39.85	1.18	0.47
	Tenn.	6	3 926 018	107 141	36.64	1.53	0.56
	Va.	5	4 651 448	103 180	45.08	1.07	0.48
	Ga.	3	4 587 930	150 730	30.44	0.65	0.20
	Md.	3	3 923 897	25 592	153.33	0.76	1.17
	Miss.	2	2 246 994	122 657	18.32	0.89	0.16
	Ky.	2	3 220 711	103 214	31.20	0.62	0.19
	S.C.	1	2 590 713	78 425	33.03	0.39	0.13
	Fla.	1	6 791 418	140 212	48.44	0.15	0.07
	Ark.	0	1 923 322	135 133	14.23	0.00	0.00
	Ala.	0	3 444 354	131 704	26.15	0.00	0.00
	La.	0	3 644 637	116 951	31.16	0.00	0.00
	Southeast general	17					
	Southeast total	63	47 760 090	1 404 402	34.01	1.32	0.45
Midwest	Wis.	36	4 417 821	141 062	31.32	8.15	2.55
	Mich.	30	8 881 826	147 156	60.36	3.38	2.04
	Ont.	17	7 703 100	891 198	8.64	2.21	0.19
	Ohio	16	10 657 423	106 226	100.33	1.50	1.51
	Iowa	14	2 825 368	145 154	19.46	4.96	0.96
	Mo.	11	4 677 623	178 829	26.16	2.35	0.62
	Minn.	6	3 806 103	205 330	18.54	1.58	0.29
	Ill.	3	11 110 285	144 716	76.77	0.27	0.21
	Ind.	0	5 195 392	93 730	55.43	0.00	0.00
	Midwest general	4	0				
	Midwest total	137	59 274 941	2 053 401	28.87	3.19	0.67
Plains	S.Dak.	8	666 257	196 723	3.39	12.01	3.39
	Sask.	4	926 200	651 903	1.42	4.32	0.06
	Nebr.	4	1 485 333	198 208	7.49	2.69	0.20
	Man.	2	988 200	650 090	1.52	2.02	0.03
	N.Dak.	0	617 792	179 435	3.44	0.00	0.00
	Kans.	0	2 249 071	212 525	10.58	0.00	0.00
	Plains general	1					
	Plains total	19	6 932 853	2 088 884	3.32	2.74	0.09
Rocky Mountain	Wyo.	62	332 416	251 958	1.32	186.51	2.46
	Utah	38	1 059 273	213 367	4.96	35.87	1.78
	Mont.	31	694 409	377 112	1.84	44.64	0.82

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Table 3. *concluded.*

Region	State or province	No. of articles	Population in 1970–1971	Area (km^2)	Population density (no./km^2)	Articles per million people	Articles per 10 000 km^2
	Idaho	31	713 015	214 133	3.33	43.48	1.45
	Colo.	29	2 209 596	268 834	8.22	13.12	1.08
	Alta.	5	1 627 900	661 188	2.46	3.07	0.08
	Rocky Mountain general	10					
	Rocky Mountain total	206	6 636 609	1 986 592	3.34	31.04	1.04
Southwest	N.M.	14	1 017 055	314 543	3.23	13.77	0.45
	Ariz.	4	1 775 399	294 128	6.04	2.25	0.14
	Nev.	4	488 738	284 613	1.72	8.18	0.14
	Tex.	3	11 198 655	681 092	16.44	0.27	0.11
	Okla.	2	2 559 463	178 669	14.33	0.78	0.14
	Southwest general	15					
	Southwest total	42	17 039 310	1 753 044	9.72	2.46	0.24
Pacific Coast	Oreg.	75	2 091 533	249 181	8.39	35.86	3.01
	Calif.	63	19 971 069	405 431	49.26	3.15	1.55
	B.C.	32	2 184 600	948 600	2.30	14.65	0.34
	Alaska	21	302 583	1 479 058	0.20	69.40	0.14
	Wash.	18	3 413 244	172 657	19.77	5.27	1.04
	Yukon	0	18 400	536 327	0.03	0.00	0.00
	Pacific general	24					
	Pacific total	233	27 981 429	3 791 255	7.38	8.33	0.61
Hawaii	Hawaii	3	769 913	16 615	46.34	3.90	1.81

fishery program's top priorities and has developed strategies to meet those objectives (Taylor 1995).

Because wild populations depend on suitable environmental conditions, managing for wild fish is habitat based. Thus, wild fish policies and programs heavily involve habitat work in addition to local cessation of stocking and to setting special angling regulations (Vincent 1991). This trend bodes for increased emphasis on habitat management in the programs of fishery resource agencies.

Emphasis on prevention and self-healing

Indications are that the effectiveness of managing stream habitat for fish will lie increasingly in habitat protection, i.e., preventive management, and in restoring habitat by putting nature in position to do most of the work by regenerative processes. Much preventive management for stream habitat is embodied in law and in policies of agencies that regulate natural resource use. Such laws and policies have obviously become increasingly protective, especially since 1970. For example, in the last 30 years or so, British Columbia's forestry planning progressed from no role for fishery managers, to a referral reception role, to "folio planning" (map overlay team procedure on influences of soils, land forms, etc. related to logging and streams), to more fully integrated land-use planning that includes legislation for a forest practices code (P.A. Slaney, B.C. Fisheries Branch, Vancouver, B.C., personal communication). Much of the reform derived from long-term studies of forestry practices and salmonid habitat at Carnation Creek, British Columbia, synthesized in Hartman and Scrivener (1990).

The trend toward emphasizing natural processes is represented by papers in Meehan (1991) and in Naiman (1992), and by the stream restoration manuals of Newbury and Gaboury (1993) and the Ontario Ministry of Natural Resources (1994). In the natural, regenerative approach, managers recognize their overall task more as people management than as fish management, influencing human behavior so that people damage fish habitat less. Thus, the most productive trend in stream habitat work will probably be toward preventing, reducing, and removing anthropogenic causes of deterioration and letting natural interactions of vegetational regrowth, hydraulics, and sediment redistribution improve and maintain habitat.

On the other hand, some of the artificial restructuring of channels that characterized the field's past will likely remain important, especially where natural regeneration would require decades, even centuries. For example, natural recovery of structural habitat tends to be unacceptably slow after channel straightening (Gebhards 1970) or where streams were used for driving logs or railroad ties to mills. Also, reconstruction may often be needed where rapid repair from abused conditions is essential for recovery of endangered fish populations. Managers continue to develop and refine in-channel techniques, and manuals continue to appear (Hunter 1991; Hunt 1993) that present significant advances and will help much in raising the effectiveness of instream habitat work.

Managing with ecological wisdom for healthy biotic communities will benefit streams and fish immensely. Concepts of biotic integrity (Karr 1991; Angermeier and Karr 1994), ecosystem health (Costanza et al. 1992), and comprehensive ecological philosophy (Botkin 1990) are strongly influencing such approaches. Karr (1991) advocated broad-scale environmental management in remedying human-induced impacts on aquatic ecosystems, including attention to (1) food sources, (2) water quality, (3) habitat structure, (4) flow regime, and (5) biotic interactions.

Health, an elusive but important concept, creates unease in those who view the world mechanistically. A biotic system is healthy when its inherent potential is approached, its condition is "stable," its capacity for self-repair is intact, and external

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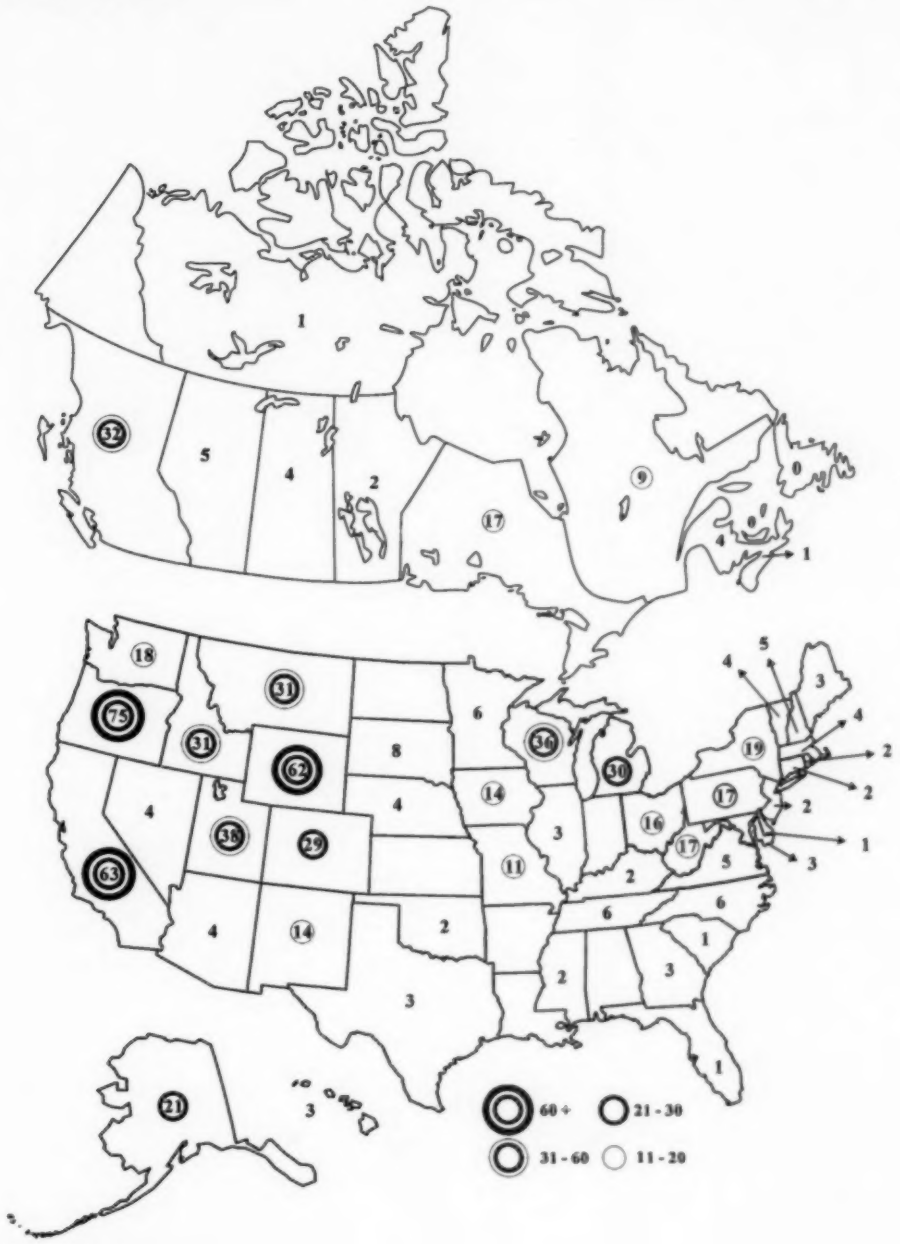
Fig. 6. Spatial distribution of those North American stream-habitat-related articles in Duff and Banks (1988) for which the subject state or province could be identified. $N = 706$.



support for its maintenance is minimal (Neess 1974; reiterated in Karr et al. 1986; Karr 1991). We should avoid the mistake of those physicians who, in focusing on disease and treatment, forget health.

Effectiveness, maintenance, and neglect

Evaluation of habitat management has generally been considered inadequate (Hall and Baker 1982; Reeves and Roelofs 1982; Hall 1984; Reeves et al. 1991*b*), and recently, Everest et al. (1991) and Reeves et al. (1991*a*) advised on how to evaluate better. However, habitat work has probably been evaluated far more and better than hatchery-based fishery work, especially in terms of the funding ratio of operations to evaluation. The several-decade history of stream habitat work

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Fig. 7. Spatial distribution of those pre-1970 North American stream-habitat-related articles in Duff and Banks (1988) for which the subject state or province could be identified. $N = 190$.

affords a record of physical and biological changes after projects.

Thorough review of evaluations is beyond this paper's scope, but I cite some that may bracket the general situation. Hunt (1988) summarized 45 Wisconsin evaluations of trout population responses to structural habitat work involving in-channel constructions or manipulation of bank vegetation. He found some techniques (e.g., Wisconsin-style deflector-bank covers) more effective than others. Among six response variables (number of trout, number 15 cm or longer (legal size), number 25 cm or longer (quality size), total biomass, angler hours, and harvest, not all of these measured in most studies), at least one variable improved in 93% of 41 treatment sections containing wild trout. Average post-treatment changes for the 41 wild trout treatment sections included increases of 21% in number of trout (to 1205/km), 35% in legal-sized trout (to

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Fig. 8. Spatial distribution of those 1970–1988 North American stream-habitat-related articles in Duff and Banks (1988) for which the subject state or province could be identified. $N = 441$.

514/km), 56% in quality-sized trout (to 97/km), and 49% in trout biomass (to 68 kg/km). In addition, some evaluations of stream habitat work in Michigan found positive trout population responses (Shetter et al. 1949; Latta 1972), and favorable results in Wyoming spring creeks is well known (Binns 1986, 1990, 1994; Binns and Remmick 1994).

Positive effects also derive from habitat work in somewhat steeper spring creeks. In four Wisconsin creeks having gradients of 1–1.4%, seven of eight types of instream habitat structures tested had favorable effects on the trout populations (Hunt 1992).

More mixed results come from evaluations of structural manipulation of high energy streams of steeper landscapes. As reviewed by Hamilton (1989), studies in Pacific drainage streams where winter precipitation is heavy include some (Ward and Slaney 1979, 1981; Overton et al. 1981; Moreau

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1984; West 1984; House and Boehne 1986) reporting favorable results and others (Barnhart et al. 1983; Everest et al. 1984; Petrosky and Holubetz 1985; Fontaine 1987) that failed to show significant fishery benefits. Regardless of the physical or biological responses, most studies gave clues for improving later work.

Recent West Coast evaluations continue to produce varied findings. Ongoing U.S. Forest Service studies of habitat work in Fish Creek, Oregon, are generally inconclusive (Everest et al. 1988). In an unusually steep (3.8%) second-order California stream, winter high water destroyed or severely damaged 86% of 37 rock deflectors (inadequately designed and built, and having questionable objectives, e.g., to increase water velocity in such a stream), and effects of the structural work on juvenile steelhead (*Oncorhynchus mykiss*) were neutral to negative (Hamilton 1989). In contrast, House et al. (1989) reported 8-yr evaluations showing that rehabilitation work in Oregon Pacific slope streams achieved structural, biological, and economic success; the best and probably least costly method was riparian management to provide optimum numbers of all sizes of streamside conifer trees.

Literature reviewed by Hamilton (1989) indicated that salmonid populations generally declined or showed no change after structural habitat work in streams having gradients of about 2% or more, whereas success was much surer in gradients of around 1% or less. In view of the lessons from past work, a team having proper expertise in hydrology, geomorphology, stream-fish ecology, and construction or management skills should be able to design and implement appropriate habitat treatment (which might be no treatment) in most any salmonid stream having less than 2% gradient.

To those who question habitat work in general because some projects had poor results, it can be said that failed habitat projects are simply ones not properly designed or built. We are still in this field's early learning stages. Much learning must be by trial and error, and some of the errors will remain for people to view. Also, the managers vary in skill. Beneficial work requires direct supervision from qualified professionals. Inept stream manipulation by well-meaning but poorly grounded agency personnel and by laypersons has long been a problem. Added to this in the last 20 yr or so has been activity of a few "habitat improvement" impostors among private consultants. Waste and harm are caused by managers so infatuated with tools and techniques that they confuse means and ends, losing sight of objectives (White 1991). The purely tactical manager, who applies methods with little understanding of how streams and the life in them function, is a danger.

How long can even a successful habitat project keep functioning as intended? This depends not only on design, materials, and skill of construction, but also on appropriate, ongoing maintenance. To the degree that instream work is artificial rather than naturally developed, it usually must be frequently inspected and maintained, if it is to last. This is especially so in streams subject to forceful high water. Maintenance of constructed habitat projects is often deficient because it tends to be unappealing compared with construction, and poor continuity of agency personnel and administrative apathy exacerbate the neglect. For example, since the 1950s, the state of Wisconsin has treated several miles of trout stream each year by instream structural methods, a program widely regarded as exemplary. However, even some of the better designed and built projects, which should have lasted a century or more, deteriorated severely in 25 yr or less because they did not receive the small amount of annual inspection and adjustment required to maintain durability. Besides disintegration, some projects in low-gradient streams are rendered nonfunctional by excessive accumulations of woody debris that impound the channel (author's observations and discussions with Wisconsin managers). Similar neglect is evident in other jurisdictions. Where natural healing can be used instead of construction, maintenance needs will probably be much reduced.

Importance of woody debris

In the trend toward self-restorative approaches in habitat work, consideration of the roles of wood material in channels and riparian areas has increased. Wood of all sizes and origins is recognized as important, but the LWD school of stream habitat study and management predominates (Keller and Swanson 1979; Lisle 1981; Gregory et al. 1991; Hicks et al. 1991; Sedell and Beschta 1991; Gregory and Davis 1992; Fausch and Northcote 1992; Ralph et al. 1994). LWD affects channel form, transport and deposition of sediment, retention of organic matter, and the composition and functioning of the biotic community (Naiman et al. 1992). Generally classed as LWD is fallen woody material (logs, root masses, limbs) >10 cm diameter and >2 m long, but functional definitions of woody debris vary according to stream size (Bilby and Ward 1989). Rather than an arbitrary size classification, the LWD roles in streams are what matter to fish. The LWD size continuum should be extended downward for smaller streams or for small-scale processes in any stream (Richmond and Fausch 1995).

LWD interest began in the East well before 1988 (Bilby 1979), and Angermeier and Karr (1984) analyzed woody debris and fish habitat relationships in a warmwater stream there, but the subject developed most vigorously in connection with high-energy streams of the Pacific Coast rain-forest mountains. The parts of such streams in old-growth coniferous forest are often log dominated, the beds, banks, and riparian zones thatched with layers of large (often >1-m diameter) fallen trees, intermixed with gravel, other soils, and live vegetation. This resists erosion by powerful high water, which usually occurs in winter. During the region's characteristic summer drought, the dense forest and fallen-tree complex ameliorates streamflow diminution and warming and provides abundant hiding cover and other structural habitat for salmonids.

Harvesting West Coast forests and removing LWD from channels for log-drive transport, agriculture, and urbanization devastate salmon and trout production. An important management change was halting of agency programs that prevailed in the 1960s and 1970s to remove log jams and other wood debris from western streams, especially after logging (Ralph et al. 1994). Forest harvest effects in decreasing supply of wood to streams are much studied (reviewed in Hicks et al. 1991). Ralph et al. (1994) measured LWD and channel morphology of western Washington streams in old growth and in forest harvested at different intensities, finding that changes due to logging damaged salmonid habitat. Hartman and Scrivener (1990) studied physical and biological results of forest harvest in a West Coast stream, finding positive, neutral, and negative effects; the latter predominated in terms of habitat features and reduced salmonid production.

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Agencies developed methods for rehabilitating such ruined channels by artificially installing LWD (House and Boehne 1985, 1986; House et al. 1989, 1991; House and Crispin 1990; Armantrout 1991), and they promote forest management for riparian regrowth to naturally regenerate LWD and restore structural complexity and stability in streams (Beschta 1991; Reeves et al. 1991*b*; Sedell and Beschta 1991). A slogan of that movement is "Manage for the mess!"

For natural regeneration of LWD in stream channels, Sedell and Beschta (1991) recommend the following:"(1) encourage and promote the growth of important riparian species, (2) provide woody vegetation along stream channels that helps maintain important riparian functions and groundwater levels, (3) allow plant succession to occur relatively unhindered, and (4) [choose for such management] reaches within a basin that not only are important for fish but are where the stream has its greatest interaction with streamside vegetation. Areas where flowing water interacts strongly with riparian vegetation and adjacent terrain are typically the areas that have the most diverse and productive habitats. Vegetation is less costly than other habitat structures and provides a more complex and functional habitat."

Such principles and methods apply in regions having other climates, terrain, flow regimes, soils, vegetation, and fishes but need adjustment there. Channel-spanning LWD (log jams, beaver dams) cause essential pools and gravel deposits to form in steep, cool-climate streams of the Pacific Coast, but LWD can so slow flow in creeks of the southern Great Lakes region that scarce spawning gravels become buried in sand and silt, and water becomes too warm for trout in summer. Therefore, spanning LWD structure is promoted liberally in the former region and sparingly in the latter.

Stream-edge LWD provides superb hiding and feeding cover for fish in many streams. Dense fringes of tag alder (*Alnus rugosa*) debris lining edges of slow, sand-bedded creeks can displace the meander-bend thalweg to midchannel, inhibiting formation of lateral-scour pools that harbor trout (Hunt 1979), but in general, partially submerged LWD lodged along outer banks of meander-bend pools in spring creeks, promotes optimal channel form and essential hiding–security cover. Indeed, in their early manual on trout stream improvement in Michigan, Hubbs et al. (1932, p. 8) reported "resnagging" with felled trees and the like as the first official stream habitat work that Jan Metzelaar undertook in 1927. Later designs for cover structures for spring creeks often incorporated or simulated LWD accumulations (White and Brynildson 1967; Hunt 1993).

Beaver provide LWD and finer debris to stream channels. Using (or controlling) beaver in salmonid habitat work requires differing approaches in different regions and terrains. Their damming can form excellent habitat for salmonids in steep terrains but harm such fish in low-gradient streams. Much study of how beaver influence stream ecology and fish habitat developed recently (Parker et al. 1985; Naiman et al. 1986, 1988; none of which listed in Duff and Banks 1988).

Ur ban stream work

Urban sprawl has degraded water quality and structural habitat via such anthropogenic processes as channelization, culverting, riparian vegetational destruction, sediment flow from construction, creating impervious surfaces (intensifying stormwater runoff), and other hydrologic change. Lucchetti and Fuerstenberg (1993) reviewed urban "development" effects on salmon streams, particularly the dramatic alteration of watershed hydrology, loss of LWD, water quality effects, and radical restructuring of channels into unnatural shapes. They emphasized the important general consequences of environmental stress on biotic communities (Gray 1989), such as (1) reduced efficiency of ecosystem processes, (2) increased flow of nutrients from terrestrial to aquatic systems, (3) shifts in the biota toward organisms that are short lived, small, exotic, and characterized by high reproductive rates, and (4) retrogression to earlier stages of ecological development in which self-regulatory functions are less developed and species diversity is reduced (Rapport 1989). Lucchetti and Fuerstenberg (1993) concluded that some kinds of restoration (e.g., replicating old-growth forest conditions) are precluded in most urban streams and that suitable methods include reducing hydrologic impacts, encouraging redevelopment of complex riparian zones, and installing LWD. They indicated much of this can benefit humans by reducing flooding, erosion, and water quality problems. Further elaboration of urban stream habitat problems is in Klein (1979), Richey (1982), ARC (1986), Galli (1990), Booth (1991), Booth and Reinelt (1993), and Booth and Jackson 1994).

Cognizance of geomorphology

Another trend in stream habitat work is increased use of geomorphology, besides the hydrology that has long played a part. Fluvial geomorphologists provided technical reference (Leopold et al. 1964; Dunne and Leopold 1978; Newbury and Gaboury 1993; Leopold 1994; OMNR 1994) essential for habitat managers and played roles in developing LWD awareness. Salmonid spawning gravel analyses by Kondolf and Wolman (1993) and Kondolf et al. (1993) illustrate how geomorphologists can contribute habitat information. A stream classification scheme based on morphology (Rosgen and Fittante 1986; Rosgen 1994) helps in recognizing features and standardizing terms, but geomorphologists caution about its limitations and point out that working with geomorphic processes requires deeper understanding than typology.

Watershed, landscape, and ecosystem scales

Emerging programs of watershed (or drainage-basin) restoration and protection are perhaps the newest development. Schlosser (1991) advocated understanding processes at the landscape level of biological organization to manage fish. This represents resurgence of a trend of the late 1940s into the 1960s, which faded largely due to landowner inconvenience and apathy. The envisaged watershed approach, integrating hydrology, fluvial geomorphology, plant ecology, soil science, and other fields (exemplified by papers in Naiman 1992), is resurging in part because it offers solutions to dilemmas inherent in the idea of "ecosystem management." Defining what ecosystems are, or delimiting them, presents much difficulty. The watershed has emerged as an identifiable and meaningful ecosystem unit, which may prove practicable in management.

Doppelt et al. (1993) put forth a bold plan for applying ecological management on a watershed scale in Pacific Northwest. They maintained that the dynamic character of aquatic systems must be protected and restored, not just specific habitat components and conditions. They proposed that, to con-

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serve and expand anadromous salmonid habitat, (1) top priority be given to protecting intact watersheds, (2) restoration of damaged watersheds be of secondary but still important priority, and (3) within the range of those degraded watersheds, the ones that have been damaged least should have restoration priority. The last point counters previous professional opinion. Stream habitat scientists and managers have felt that the greatest restoration gain per dollar spent usually derives from treating severely degraded habitat that nonetheless holds potential for recovery. Testing the two strategies against each other should be interesting.

More comprehensive objectives

Rising ecological awareness has broadened program objectives of natural resource agencies. Within this trend, biodiversity and the more useful concept of biological integrity have become issues in managing for ecosystem health and in offering a wider array of recreational opportunities than in the traditional fishery agency mission. Biodiversity involves numbers of forms present in an area, not only as species, but also at such organizational levels as genes and ecosystems, whereas biological integrity "refers to a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates" (Angermeier and Karr 1994). Goals of biotic integrity and ecological health are stated or implicit in the U.S. Clean Water Act, Canada's National Park Act, and Ontario's strategic fisheries plan (OMNR 1992).

The new policies on biological diversity, integrity, and health pose challenges for those fishery managers accustomed to providing a narrow range of "target" sport- and food-fishes and facing strong demand from fishers for those few species. Reforming habitat management toward meeting criteria of biological integrity will involve considering the needs and functions of the entire biota native to the managed site and non-native species where they are valued or unavoidably established. Biodiversity in the form of numerous non-native species is largely inconsistent with biological integrity of an ecosystem (Angermeier and Karr 1994).

Included in the trend toward broader biological management is management of stream habitat for non-salmonids. Relatively little habitat work has been done for fishes in warmwater streams, but the practice is growing. Lyons and Courtney (1990) reviewed 22 habitat projects (some unpublished) encompassing 42 U.S. streams, examined information on trout habitat work for applicability to warmwater streams, and made recommendations for starting projects. They emphasized revegetation for streambank stabilization but considered structural methods for increasing instream cover in certain situations.

The challenge of doing justice to biological integrity may be less daunting in managing stream habitat for salmonids than for non-cold-water fishes. Typically, the native fish communities of salmonid streams have far fewer species than do warmer water fish communities, particularly in the small waters where habitat work is most appropriate. However, managing habitat for any native fish stock in keeping with natural stream processes will probably benefit also the normally associated biota.

Management implications

The literature reveals habitat management as a restorative field of applied ecology involving strong aspects of protection. Restoration is usually most effective in the long run if done in ways that promote natural regenerative processes, i.e., putting streams, and thereby fish populations, in position to restore themselves via self-healing powers of nature. It will be most beneficial to regard stream habitat work less as reconstruction than as healing. To be protected above all is habitat that remains in healthy natural or seminatural condition. Letting habitat be destroyed in one place while exerting effort to restore it elsewhere in the same jurisdiction is shortsighted but often prevails because of sheer inefficiency and temptations to avoid difficult responsibility and expand bureaucratic activity. Vigilance is also needed to protect habitat that has been significantly restored toward previous good condition.

As habitat work is primarily restorative, it will be well for managers and agencies not to let the idea of restoration become perverted (and the public confused) by term twisting or by activities that detract from the concept. Examples are bank stabilization or flood control projects, such as levees, rip-rap, or concrete walls, intended to protect floodplain land or buildings (which should have been built elsewhere) against natural migration of stream channels, or removing woody debris for navigation or flood-control purposes, then calling these efforts "restoration" or even "habitat restoration."

Another example is the largely illusory idea of "restoring" wild trout and salmon populations by stocking hatchery-produced fish instead of attending to the problems of overfishing and habitat destruction that caused the decline (White 1992*a*, 1992*b*). Restorative stocking is warranted only where the population cannot self-regenerate after the habitat or harvest causes of its demise have been remedied, and even then it should be needed only as a temporary measure (White et al. 1995*a*).

Also the very concept, ecosystem management, has a disturbing ring. It seems arrogant to talk of managing ecosystems, which are not mere corn fields or tree farms. Especially where we work at the moderate-to-large watershed scale (say, 100 – 100 000 km^2) and, especially if those areas embody biotic integrity, the ecosystems are probably so complex (unlike monocrop agriculture) as to be unmanageable at the intensities of control that people tend to envisage. The main consideration that puts such arrogance in perspective is the tendency (adaptation, if you will) of natural ecosystems to manage themselves well. This is especially true of the biotic components of the ecosystems. A watershed's native organisms and their interrelationships have been evolving for eons and generally do well until people interfere.

Rising concern among anglers and the broader public for wild fish and naturalness of the environments in which they thrive requires that fishery managers, besides stewarding fish populations and habitats, share values that anglers hold for fish and other organisms (importantly benthic invertebrates), for land- and water-scapes, for opportunities to use diverse fishing gear, and so on. Managers can do this only by taking part in the sport they are expected to serve. Related concerns derive from greater ecological awareness among the public, thus nonanglers' values of aquatic resources must also be shared. Recognition of human values in habitat work may be increasing, a growth beyond narrow focus on production of more fish and bigger fish.

Bottom (in press) proposed that we speak of management

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for fish, rather than of fish management, which implies management of fish. Likewise, I suggest that on a broader scale, we think not in terms of ecosystem management but of managing for ecosystems. This will mean managing human affairs to give ecosystems better chances to do what, I would submit, they do best.

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Predicting important lake habitat variables from maps using modern modelling tools

Lars Håkanson

Abstract: The aim of this work is to present several new lake management models for small, glacial lakes. The models are driven by simple, readily available "map parameters" describing the catchment area (like the percentage of mires, lakes, and forests) and the lake (area, volume, mean depth, etc.). The first step is to predict important limnological state variables (pH, total P, and colour); the second step involves predicting state indices describing the abundance of key functional groups (fish, phytoplankton and bottom fauna) and indices of special interest in lake management (Secchi depth and toxins in fish used for human consumption); and the last step concerns the definition of a lake ecosystem index based on the state indices. The ecosystem index characterizes the entire lake over extended periods (months to years) and not specific sites or sampling events. Lake indices can be obtained for a region or a country and the development can be illustrated with trend analyses. If these trends are linked to remedial measures, the effect of the remedies can be discussed qualitatively and quantitatively in terms of cost-benefit analyses. Calculations like this use Geographical Information Systems together with regional models based on map parameters.

Résumé : Ces travaux ont pour but de présenter plusieurs nouveaux modèles de gestion des petits lacs glaciaires. Les modèles sont régis par des paramètres «cartographiques»+ simples et faciles à obtenir qui décrivent le bassin récepteur (comme la proportion de tourbières ombrotrophes, de lacs et de forêts) et le lac (superficie, volume, profondeur moyenne, etc.). La première étape consiste à prédire des variables d'état limnologiques importantes (pH, P total et couleur); la deuxième consiste à prédire les indices d'état décrivant l'abondance des principaux groupes fonctionnels (poissons, phytoplancton et faune benthique) et les indices auxquels on s'intéresse tout particulièrement dans la gestion des lacs (transparence mesurée au disque de Secchi et toxines présentes chez les poissons destinés à l'alimentation humaine); la dernière étape consiste à définir un indice de l'écosystème du lac à partir des indices d'état. L'indice de l'écosystème s'applique à la totalité du lac sur des périodes prolongées (s'échelonnant sur des mois ou des années) et non à certains endroits ou moments où des échantillons ont été prélevés. On peut obtenir ces indices pour une région ou un pays et illustrer leur évolution au moyen d'une analyse des tendances. En reliant ces tendances à des mesures correctrices, on peut juger qualitativement et quantitativement des effets de ces mesures au moyen d'analyses cofts-avantages. De tels calculs font appel aux systèmes d'information géographique (SIG) alliés aux modèles régionaux fondés sur des paramètres cartographiques. [Traduit par la Rédaction]

Introduction

Hedendorf et al. (1992) identified important relationships among abiotic and biotic lake variables. The habitat question is how the abiotic (geographical, geological, topographical, etc.) conditions of the lake and its watershed influence and interact with important, key functional groups of the lake ecosystem. I will address the quantification of such relationships. It is easy to argue that all physical, chemical, and geological factors could influence lake metabolism. But how can such statements be brought to a higher level of analysis where the factors are not just identified but also quantitatively ranked and utilized in predictive management models? Such models must be driven by simple, readily available model variables (x), the models must be validated against reliable empirical data, and the predictive power and uncertainty limits of the predictions should be given (Håkanson and Peters 1995).

The basic idea of this paper is to compile models in steps from simple, geological "map parameters" describing the catchment area, via important limnological state variables to a lake ecosystem index (LEI) based on the abundance of key functional groups (Fig. 1). Several new models and approaches will be presented. Note, however, that these results do not apply to all lakes on earth. The models are valid for small, glacial lakes. There are about 83 000 lakes in Sweden, about 81 000 belong to this lake type. Similar proportions ought to apply also for Finland, Russia, Canada, and the northern United States. So, this is the most common lake type on earth. Many of the methodological principles that apply for these lakes ought to apply also for other types of lakes, and to other ecosystems, like rivers and forest ecosystems.

Defining ecosystem boundaries and model presuppositions

In this approach, it is important to define the fundamental unit, the lake ecosystem. This is not a diffuse food-web structure, but a defined geographical area. Large lakes may have to be separated into sub-ecosystems where different key organisms dominate. Smaller lakes (area <10 km^2), like those discussed in this work, can often be regarded as single ecosystems. If a given y-variable (a key functional organism, a limnological state variable, etc.) varies more within a defined ecosystem (like a lake) than among ecosystems, it becomes very difficult

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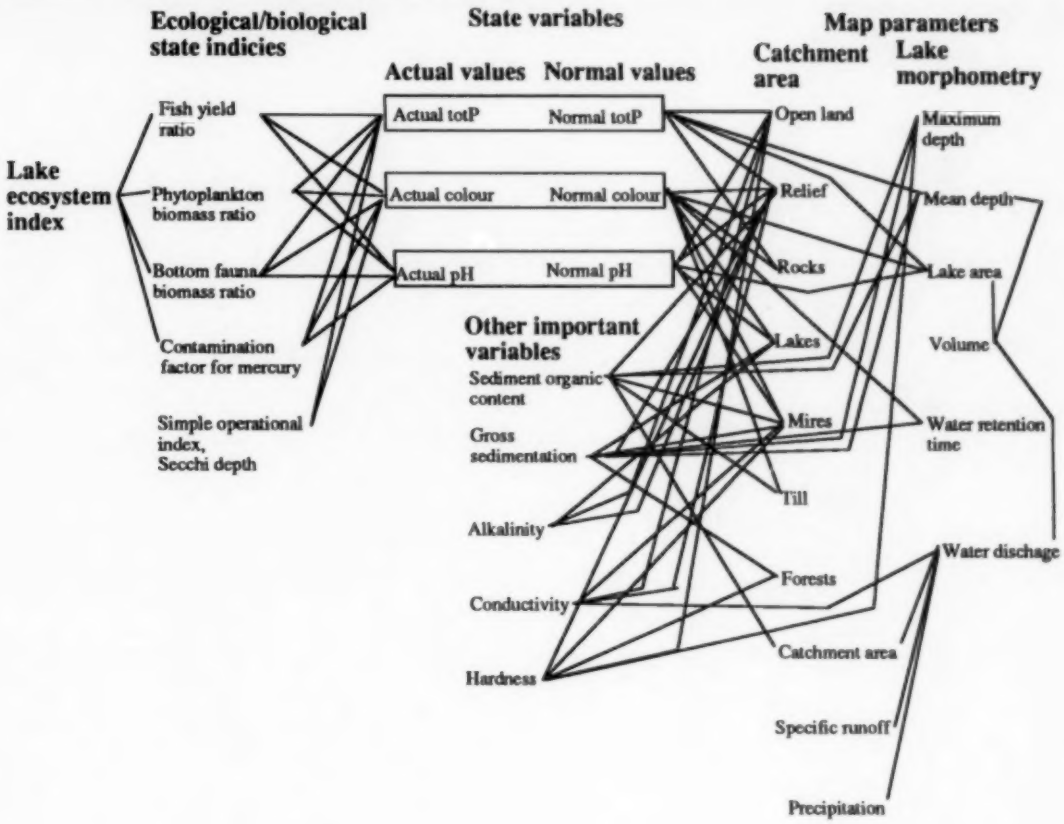
Fig. 1. Interactions among the basic components of the lake ecosystem index.



to develop models that predict the variable. Such cases may arise where the definition of the boundaries of the ecosystem are ecologically inappropriate. An ecosystem is presumably a rather uniform entity with respect to its defining characteristics.

The variability of an ecologically important *y*-variable within an ecosystem, CV_w, may be defined by the coefficient of variation (= relative standard variation, CV = SD/MV, where MV is the mean value and SD is the standard deviation) based on data from the given lake. The variability among ecosystems (= lakes), CV_a, may be defined from the coefficient of variation of data from different lakes (Håkanson and Peters 1995).

CV_w and CV_a have been determined for monthly data for 10 standard limnological variables for Swedish lakes (Fig. 2). As expected from this geographically restricted area of the world, there are no significant differences between CV_w and CV_a for water temperature (the ratio CV_a/CV_w is 1; Fig. 2A), so there is little purpose to developing a predictive model for the mean monthly lake temperature in these lakes based on map parameters from the catchment. In contrast, the ratios for pH, colour, alkalinity, lake total P, Secchi depth, conductivity, Fe and Ca concentration, and hardness are much higher. The greatest differences in CV_a and CV_w exist for conductivity and Fe; the smallest (except temperature) are for pH and alkalinity. The larger this ratio, the easier it usually is to build models to predict the characteristics of individual lakes. This paper gives many predictive empirical, statistical regression models for these lake variables based on map parameters from the catchment and the lake. Figure 2B shows that the best models are obtained for variables showing the highest among/within ratio and vice versa.

How should one define the ecosystem so that map parameters, like mean depth, are relevant as model variables? The problem is illustrated in Fig. 3B using data on Secchi depth (the *y*-variable to be predicted in this example; Secchi depth is a simple, useful operational measure of water quality) and mean depth (D_m, the *x*-parameter that reflects, for example, resuspension processes). For small lakes, there exists a significant ($r^2 = 0.38$, $p = 0.0001$ for 88 Swedish lakes smaller than 10 km^2) positive relationship between D_m and Secchi depth: the deeper the lake, the larger the bottom areas beneath the wave base, the less resuspension, the less suspended materials in the lake water, the clearer the water, and the larger the Secchi depth. This is logical. The mean depth has a significant meaning for an important ecosystem variable, Secchi depth. The entire lake is the defined ecosystem.

But how would this apply for a coastal area in a large lake? Is there a method to define the boundaries and establish coastal ecosystems where morphometric parameters like the mean

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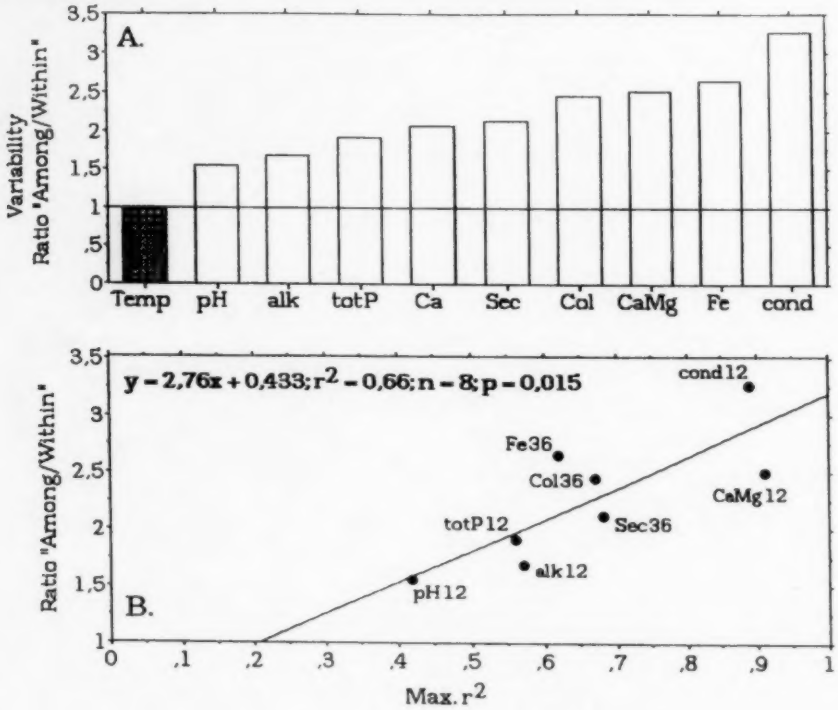
Fig. 2. (A) The ratio of within lake variability to among lake variability for 10 standard variables based on monthly data from 24 Swedish lakes. (B) The relationship between the among/within ratio and the maximum r^2-values obtained for empirical regression models (from Håkanson and Peters 1995).



depth has a meaning? This is illustrated in Fig. 3A. In this example, there are three boundary lines, A, B, and C. The mean depths of the enclosed areas are 4.5, 3.5, and 2.5 m, respectively. The exposure of the coastal area is the ratio between the section area and the three-dimensional water surface ($E = 100\ A_t/A_b$, where A_t is the section area or the opening area towards the sea in square kilometres and A_b is the three-dimensional bottom area in square kilometres). The E-values are quite different in the three cases, 0.05 for A, 0.1 for B, and 0.2 for C, but the Secchi depth is the same in all three cases (2 m). Arbitrary borderlines can be drawn in many ways and the mean depths of such areas would be devoid of meaning in relation to a target y-variable. The approach in this work (see also Pilesjö et al. 1991) assumes that the borderlines are drawn at the topographical bottlenecks so that the exposure of the coast from winds and waves from the open sea is minimized. It is easy to use the E-value as a tool to test different alternative borderlines and define the coastal ecosystem where the E-value is minimal. If the coastal ecosystem is defined in this way, then there exists, as illustrated in Fig. 3A, a significant ($r^2 = 0.14$, $p = 0.08$ for 23 Baltic coastal areas where the tidal impact is negligible) negative relationship between Secchi depth and mean depth: the larger D_m, the more resuspension, the more suspended materials in the coastal water, the more turbid the water and the smaller the Secchi depth. This is also logical because coastal areas are by definition open to the outside sea (the section area, $A_t > 0$; if $A_t = 0$, then this is not a coastal area but a lake near the sea). For such areas, a significant portion of the materials suspended in the water can "escape" from the coastal area to the open water area or to surrounding coastal areas. This is not the case for lakes. So, coastal areas with small mean depths will generally have coarse bottom sediments with small amounts of fine materials of organic and inorganic origin causing high water turbidity when resuspended.

It is always important to define the presuppositions of any model. When and where will it apply? The definition of the ecosystem boundaries is one crucial aspect of this.

Methods and data

The lakes, methods, and data in this study have been presented in other contexts (Håkanson 1991; Håkanson and Andersson 1992), and this will not be repeated here. Considerable resources have been focused on methods to establish the representativity of the samples and the reliability of the data (Håkanson et al. 1990; Håkanson 1992).

The drainage area zonation (DAZ) method (Nilsson and Håkanson 1992) provides normalized values accounting for (*i*) the distance between the drainage area features (e.g., mires) and the target lake, (*ii*) the main direction of water flow in the drainage area, and (*iii*) the area of the drainage area features (e.g., mires). The characteristics of the catchment govern the inflow of water, ions, and suspended organic matter to the lake. Any catchment area may be described by various factors. One aim of this work is to try to quantify the relative importance of such factors in predicting important lake variables.

The following water chemical variables were determined for 95

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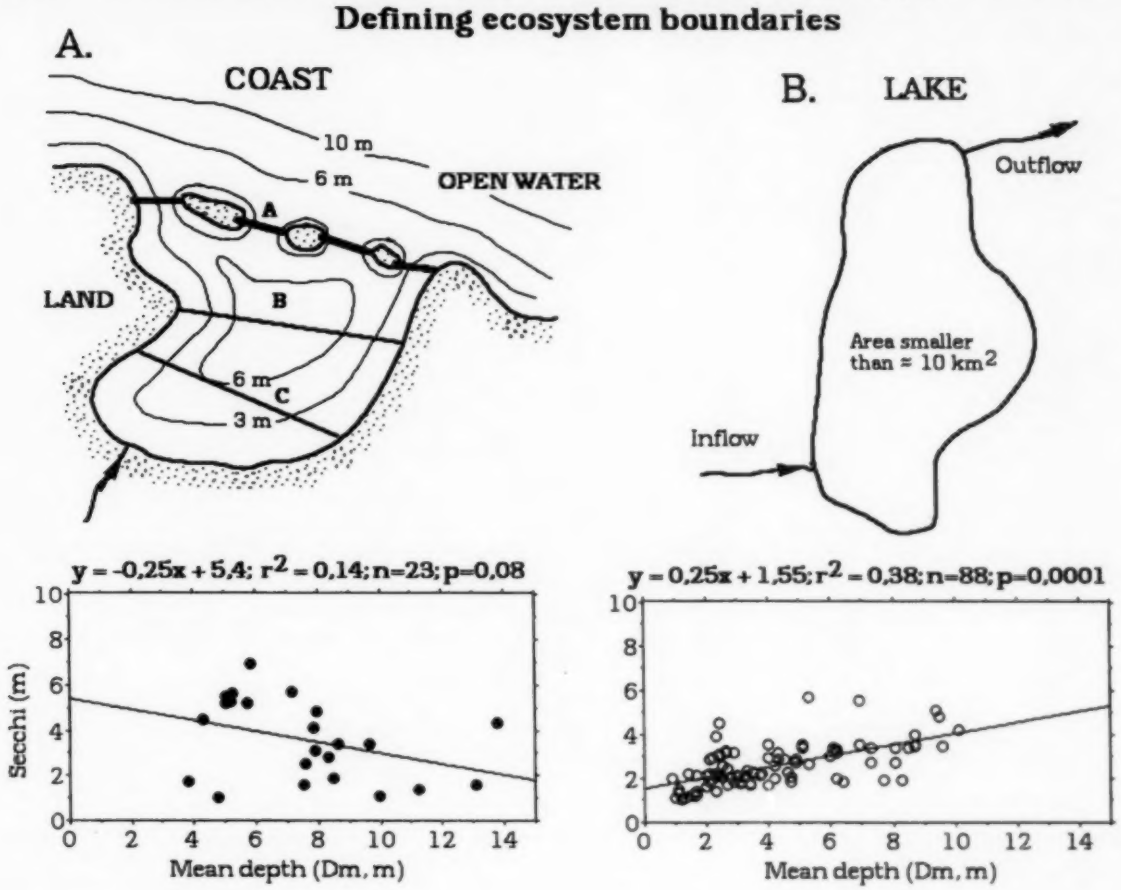
Fig. 3. Illustration and rationale for the definition of lake and coastal ecosystems by the exposure (E = the "topographical bottlenecks").



lakes for 4 yr (monthly samples from one or two central lake sites): pH, temperature, alkalinity, total P, conductivity, Fe concentration, Ca concentration, hardness (= Ca + Mg concentrations), and colour.

The empirical values of Secchi depth are mean values from monthly sampling from central sites in lakes. Data are available from 88 Swedish lakes for 4 yr.

These lakes are relatively acidic (mean pH ≈ 6), have a low bioproduction (mean total P ≈12 $\mu g \cdot L^{-1}$) and a high colour value (≈100 mg $Pt \cdot L^{-1}$). The lakes are small with a mean area of 0.8 km^2 and a mean catchment area of 16 km^2. They are also shallow, ranging in maximum depth (D_{max}) from 1.7 to 52 m. For further details about these lakes, see Håkanson and Peters (1995).

Basic concepts and rationale

Many factors related to the bathymetry and the watershed (geology, soil types, land use, etc.) could, potentially, influence lake variables, like colour, pH, and lake total P. For lake colour, Rasmussen et al. (1989) have demonstrated that, in 337 lakes from Canada and the northern United States, colour was (*i*) positively linked to the drainage ratio (the ratio between the size of the drainage area, ADA, and the lake area), i.e., ADA/area; (*ii*) negatively linked to the slope of the drainage area, i.e., steep drainage areas generally have thinner organic horizons, less bogs and mires, and a higher groundwater discharge, and mountain lakes are often exceptionally clear; and (*iii*) negatively related to lake mean depth and lake area in that the turnover of coloured substances could also be related to resuspension processes.

The best general regression model explained 60% of the statistical variance in lake colour among these American lakes. Rasmussen et al. (1989) presented several suggestions as to why certain catchment and lake morphometric parameters were influential.

It is evident that colour (and other water-quality measures) is not influenced by just map parameters, but also by the long- and short-term variations in temperature, wind and wave activity, precipitation, deposition of sulphur and nitrogen, and the type of land use. But what relative importance should one give to the catchment characteristics (bedrocks, soils, mires, lakes, forests, etc.), their distribution, and the lake morphometry? If it were possible to quantify this, then it would also be possible to say that *x*% of the variability in lake colour could be attributed to the defined map constants and the rest of the variability to, for example, climatological variables.

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Table 1. An *r*-rank table of the linear correlation coefficients (*r*) between lake colour (log(col36)) and different characteristics of the lake.

Variable	log(col36)
MireZ	0.37
Mire%	0.37
TillZ	0.31
Till%	0.30
MireN	0.30
BET	0.25
Vd	0.21
TillN	0.19
$DR^{0.1}$	0.17
$1/F$	0.11
log(1 + LakeN)	−0.15
Bm	−0.15
log(RDA)	−0.16
log(RNA)	−0.19
log(1 + Lake%)	−0.21
log(1 + LakeZ)	−0.21
ForestN	−0.21
Lake%	−0.21
I_o	−0.22
Lmax	−0.23
A_{tot}	−0.24
$area^{½}$	−0.25
BA	−0.25
log(D_{rel})	−0.27
$Forest\%^{½}$	−0.28
$ForestZ^{½}$	−0.28
$1000\ Vol^{0.1}$	−0.38
area/ADA	−0.39
log(D_{max})	−0.44
log(D_m)	−0.46
Rock%	−0.49
T	−0.49
log(1 + RockN)	−0.50
log(Fe36)[a]	0.89
log(totP12)[b]	0.64
1/(Ca3/12)[b]	0.35
log(alk3/12 + 0.01)[c]	−0.32
pH12[d]	−0.37

Note: Correlations yielding *r*-values with absolute values below 0.1 have been omitted (n = 92 unless otherwise indicated). Data are from Håkanson (1993*b*). Mire%, uncorrected percentage of mires in the catchment; MireZ, DAZ-corrected value of mires in the catchment; MireN, mires in the near area, as determined with the DAZ method. [a] $n = 28$.

[b] $n = 30$.

[c] $n = 80$.

[d] $n = 88$.

Such knowledge, and the possibility to predict and quantify, would provide a better basis for understanding causation and possible remedial strategies.

It is evident (Stumm and Morgan 1981; Wetzel 1983; Rasmussen et al. 1989) that models for colour or total P (e.g., see OECD 1982) based on water chemistry data (like Fe, hardness, and pH) may enhance the predictability of the model, but there are also drawbacks with the use of such models because: (*i*) all water chemistry parameters (*x*) vary in time and space, so one has to demonstrate which characteristic (mean, median, area-weighted mean, etc.) would be most compatible with the *y*-variable; (*ii*) it may be difficult and expensive to get access to the most relevant water chemistrry input data (*x*) for such models; (*iii*) it may be difficult to causally relate statistical measures of water chemistry (*x*) to a statistical measure of the *y*-variable; (*iv*) water chemistry parameters are highly dependent on the characteristics of the catchment and the lake (Nilsson and Håkanson 1992); and (*v*) the variability of the water chemistry parameters (pH, alkalinity, etc.) are also linked to a great number of reactions in the lake itself.

A good predictive model helps to formulate a prediction without too much work (like water sampling, laboratory analyses, measurements of water discharge, etc.). It should not be more demanding to access model (*x*) parameters than to obtain empirical data on the *y*-variables. No single factor is likely to explain, statistically or causally, the great variability in colour, pH, and total P that exists among lakes. Several factors describing the catchment area, the distribution of the features in the catchment and within the lake, ought to be included in a multivariate approach. Each factor is likely to add only a limited amount of explanation.

The state variables: colour, pH, and total P

The following section demonstrates some of the steps in the derivation of empirical models for important lake variables from simple, readily available map parameters. The procedures given in Håkanson (1991) and Håkanson and Peters (1995) are used, and this will not be discussed further.

Presuppositions and aim

The first aim is to illustrate the basic principles of the approach using lake colour as target *y*-variable. The idea is to predict long-term mean colour (col36 in milligrams Pt per litre, where 36 indicates that the mean is based data from 36 consecutive monthly samples) from readily available map parameters.

r-rank

Table 1 ranks correlates (correlation coefficients; *r*) between log(col36) and map parameters and water chemistry variables. The logarithmic transformation is used because log(col36) gives the most normal frequency distribution for this population of lakes. Table 1 indicates that RockN (i.e., the percentage of the near area of the catchment covered by rocks, as determined with the DAZ method; in the following, Rock% is the uncorrected percentage of rocks in the catchment and RockZ is a DAZ-corrected value) and theoretical lake water retention time (T in years) are rather strongly correlated to log(col36) ($r = -0.50$ and -0.49, respectively). Very high and expected *r*-values occur between log(col36) and transformations of Fe36 ($r = 0.89$) and totP12 ($r = 0.64$). The *r*-rank test can be regarded as a first screening of interrelationships of potential interest for the model derivation.

It should be noted that all other lake morphometric and drainage area parameters show rather low *r*-values with lake

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Table 2. Compilation of results from different stepwise regressions for the three state variables: lake colour (col36), total P (totP12), and lake pH (pH12) ($F \geq 4$ for all regressions).

Step	Variable	r^2	Model
			col36 versus map parameters for 92 lakes
1	RockN	0.25	$\log(col36) = 2.059 - 0.202\log(1 + RockN)$
2	*T*	0.43	$\log(col36) = 2.903 - 0.179\log(1 + RockN) - 0.9117^{0.1}$
3	Lake%	0.53	$\log(col36) = 3.15 - 0.164\log(1 + RockN) - 1.1177^{0.1} - 0.026(Lake\%)$
4	Mire%	0.61	$\log(col36) = 2.982 - 0.143\log(1 + RockN) - 1.1047^{0.1} - 0.028(Lake\%) + 0.024(Mire\%)^{0.7}$
5	Till%	0.65	$\log(col36) = 2.767 - 0.088\log(1 + RockN) - 1.1597^{0.1} - 0.024(Lake\%) + 0.029(Mire\%)^{0.7} + 0.003(Till\%)$
6	area/ADA	0.67	$\log(col36) = 2.466 - 0.102\log(1 + RockN) - 0.5717^{0.1} - 0.028(Lake\%) + 0.03(Mire\%)^{0.7} + 0.003(Till\%) - 0.671(area/ADA)^{0.3}$
			totP12 versus map parameters; based on annual data from 67 lakes
1	RockN	0.23	$\log(totP12) = 1.071 - 0.006(RockN)$
2	OLN	0.36	$\log(totP12) = 1.033 - 0.005(RockN) + 0.006(OLN)$
3	Dm	0.43	$\log(totP12) = 1.133 - 0.005(RockN) + 0.005(OLN) - 0.19\log(D_m)$
4	RDA	0.48	$\log(totP12) = 1.354 - 0.005(RockN) + 0.006(OLN) - 0.171\log(D_m) - 0.146\log(RDA)$
5	area	0.56	$\log(totP12) = 1.576 - 0.006(RockN) + 0.006(OLN) - 0.053\log(D_m) - 0.252\log(RDA) - 0.151(area)^{1/2}$
			pH12 versus map parameters; based on annual data from 95 lakes
1	OLZ	0.14	$pH12 = 5.726 + 0.374\log(1 + OLZ)$
2	Mire%	0.22	$pH12 = 5.975 + 0.307\log(1 + OLZ) - 0.015(Mire\%)$
3	area	0.29	$pH12 = 5.855 + 0.244\log(1 + OLZ) - 0.019(Mire\%) + 0.261(area)^{1/2}$
4	RDA	0.38	$pH12 = 4.938 + 0.336\log(1 + OLZ) - 0.017(Mire\%) + 0.366(area)^{1/2} + 0.508\log(RDA)$
5	LakeN	0.42	$pH12 = 4.888 + 0.37\log(1 + OLZ) - 0.017(Mire\%) + 0.378(area)^{1/2} + 0.5\log(RDA) + 0.022(LakeN)$

colour, e.g., the mean water discharge (Q) had an r-value of only 0.06. One would have expected that there would be a marked relationship between Q and colour, but there is not. The main reason for this reflects the rough estimate of Q, determined from the specific runoff (SR in cubic metres per square metre per second; see Håkanson et al. 1990), which is a constant for large parts of the country, and the size of the drainage area (= ADA in square metres, i.e., $Q = SR \times ADA$). It seems probable that there exists a relationship between colour and Q, but then Q has to be determined by frequent in situ measurements (which is costly and time consuming). Because of a weak negative r-value (–0.06) between Lake% and colour, one cannot expect that lakes "upstream" of a target lake would be efficient "colour traps" for lakes further down in the drainage area. No significant improvements in model predictability could be achieved by accounting for the zonation problem. This is rather interesting since Nilsson and Håkanson (1992) demonstrated that DAZ-corrected values significantly improved the r^2-value of models for lake pH, alkalinity, conductivity, and hardness, and Håkanson and Peters (1995) have shown the same thing for sedimentation in lakes. These results indicate that colour is a more "conservative" substance than other variables. However, it would not be correct to call colour a conservative parameter because coloured substances evidently are deposited in lakes and because lake water retention time is an important model parameter for colour.

Stepwise regressions

Table 2 relates log(col36), total P (totP12, i.e., mean annual total P), and lake pH (pH12) to several map parameters. The table shows that the most powerful predictors among the map parameters are RockN ($r^2 = 0.25$ for colour and 0.23 for total P) and Open landZ (= OLZ) for pH ($r^2 = 0.14$), that after five steps the r^2-value is 0.65 for colour, 0.56 for total P, and 0.42 for pH. Note that (*i*) it is most difficult to predict pH (which agrees with the results in Fig. 2), (*ii*) no single factor is very highly correlated with any of the state variables, and (*iii*) the last factors in the models generally increase the r^2-value very little. Models based on simple catchment factors, i.e., on Rock% and not RockZ or RockN, etc., have also been developed for the lake ecosystem index. Such models generally give lower r^2-values.

A state variable of utmost importance for life in lake ecosystems is the concentration of total P in the lake water. Phosphorus is the nutrient most often limiting lake production (Table 3). The concentration of total P can be linked to most other biological lake characteristics. The concentration of total P in the lake water is a powerful predictor in limnology. Because, however, it is laborious, costly, and time consuming to measure total P from many samples, sites, and seasons, one should ask if the variable can be predicted from simple map parameters and which map parameters would be important? Table 2 gives an quantitative answer to this question. Several of the relationships in Table 3 will be used in the derivation of the LEI.

The residual variability not accounted for by these models could be linked to deficiencies in this empirical data set and to other factors not included in the models.

Defining "natural" background values

Because so many processes influence pH, total P, and colour, the natural (pre-industrial, or precivilization) values vary from

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Table 3. Selected regressions illustrating the key role of lake total phosphorus in predictive limnology (from Peters 1986).

y-value	Equation	Range for TP	r^2	n	Units
Chlorophyll	$y = 0.073(totP)^{1.44}$	3–300	0.96	77	$mg \cdot m^{-3}$
Maximum primary production	$y = 20(totP) - 71$	8–200	0.95	38	$mg\ C \cdot m^{-3} \cdot d^{-1}$
Mean primary production	$y = 10(totP) - 79$	7–200	0.94	38	$mg\ C \cdot m^{-3} \cdot d^{-1}$
Nanoplankton	$y = 17(totP)^{1.3}$	3–80	0.93	23	$mg\ ww \cdot m^{-3}$
Phytoplankton	$y = 30(totP)^{1.4}$	3–80	0.88	27	$mg\ ww \cdot m^{-3}$
Fish yield	$y = 7.1(totP)$	10–550	0.87	21	$mg\ ww \cdot m^{-2} \cdot yr^{-1}$
Macrozooplankton	$y = 20(totP)^{0.65}$	3–80	0.86	12	$mg\ ww \cdot m^{-3}$
Zooplankton	$y = 38(totP)^{0.64}$	3–80	0.86	12	$mg\ ww \cdot m^{-3}$
Bacteria	$y = 0.90(totP)^{0.66}$	3–60	0.83	12	$mill. \cdot mL^{-1}$
Net plankton	$y = 8.6(totP)^{1.7}$	3–80	0.82	23	$mg\ ww \cdot m^{-3}$
Fish	$y = 590(totP)^{0.71}$	10–550	0.75	18	$mg\ ww \cdot m^{-2}$
Crustacean plankton	$y = 5.7(totP)^{0.91}$	3–300	0.72	49	$mg\ dw \cdot m^{-3}$
Microzooplankton	$y = 17(totP)^{0.71}$	3–80	0.72	12	$mg\ ww \cdot m^{-3}$
Blue-green algae	$y = 43(totP)^{0.98}$	8–1300	0.71	29	$mg\ ww \cdot m^{-3}$
Benthos	$y = 810(totP)^{0.71}$	3–100	0.48	38	$mg\ ww \cdot m^{-2}$

Note: Many biological variables whose determinations normally require extensive and expensive field and laboratory work may be estimated or predicted from one key abiotic state variable total P (in $mg \cdot m^{-3}$). Some variables may be predicted with great precision, others with much less. *n*, number of lakes used in the regression; ww, wet weight; dw, dry weight.

lake to lake. It is impossible to measure what the conditions used to be, but there are methods to predict what they were. For example, one can use paleolimnological methods on sediment core data (Smol 1990), but this will not be discussed here. Instead, the models based on map parameters will be used, and the aim is to present a simple method for approximation of natural pH, total P concentration and colour for a given lake. Such an approach could be of practical value in lake management, e.g., in lake liming, because it is expensive and undesirable to lime lakes to an unnaturally high pH. Elaborate process-oriented models permit accurate determinations of a natural pH (Sverdrup 1985; Warfvinge 1988), but such models apply only to well-studied lakes and catchments where adequate data of the driving variables are available.

In Sweden, the rule of thumb indicates that lakes should be limed to about 6.4–6.5 even though the natural, mean annual pH varies from about 5.5 to about 7.2 in small glacial lakes. Thus, the target pH (6.4) is only occasionally correct! Table 2 shows that about 40–50% of the variability in mean annual pH (pH12) among lakes can be linked to map parameters for lakes of this type.

The approach is shown in Fig. 4. The regression is based on empirical estimates of lake pH collected during 1986. It is established (Monitor 1986) that anthropogenic acidification has lowered regional mean pH values, but the present anthropogenic acidification ought not have influenced the percentage of the catchment in cultivated land or mires, lake area, or relief of the catchment. Had this study been done 100 yr ago, assuming morphometry and catchment characteristics were unaltered, one would have obtained a similar regression, but the line would be a step higher. The question is how large is that step?

Anthropogenic acidification affects different regions in Sweden, and the world, differently. From Monitor (1986), it may, for example, be reasonable to assume a 15% decrease in mean annual pH in southern Sweden because that region is close to the rest of Europe and to the sources of emissions from Britain, Germany, etc. In the northern part of Sweden, a 5% decrease may be reasonable. Figure 4 illustrates this approach to estimate the natural pH for lakes in central Sweden, assuming the average regional decrease in pH to be 10%. The model based on map parameters for mean annual pH (pH12) has been combined with a standard "regional contamination factor" for all lakes within a given region, to account for the effects of differences in catchment and lake characteristics, but not for other factors influencing differences in mean pH among lakes. Despite that limitation, the approach offers an advance in practical water management because it may identify more accurately ecologically relevant doses of lime.

The following sections use the same approach to estimate natural reference values for other water chemical variables (see Håkanson and Peters 1995 for further details).

Complex variables: Secchi depth

The Secchi depth is a much debated and used variable in contexts of lake management. Values of Secchi depth are easy to understand by the general public; clear waters with large Secchi depth seem more desirable than turbid waters. But for the scientist, it is a challenge to understand why certain lakes have low Secchi depth and other lakes high, i.e., to understand and predict Secchi depth, the causation, and variation in time and space. There are many factors that may influence the Secchi depth (see Preisendorfer (1986) for a survey). The three most important factors are linked to (*i*) primary production (i.e., the amount of plankton, etc. in the lake (more plankton less Secchi depth)); (*ii*) the amount of resuspended material (i.e., material resuspended from the lake bed via wind and wave activity, slope processes, etc.); and (*iii*) the amount of coloured matter in the lake (i.e., humic and fulvic substances from tributaries). This is easy to state but difficult to express quantitatively because these three factors are not independent. High resuspension leads to high internal loading of nutrients (Håkanson and Jansson 1983) and an increase in production. A high amount of coloured substances would mean a smaller photic zone and a lower production. A high input of coloured

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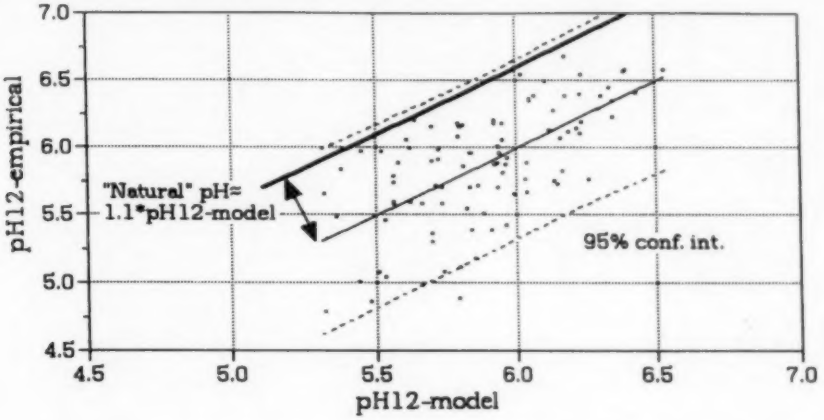
Fig. 4. A simple method to estimate the "natural" annual mean of lake pH from the model for pH12 based on map parameters The "natural" pH is given by the model-predicted pH multiplied by a regional "contamination" factor of 1.1 (i.e., it is assumed that anthropogenic acidification has decreased the pH of lakes in this region by 10% on average).



MODEL FOR "NATURAL" pH:
pHnat = RCF*pHmod

where
pHnat = predicted "natural" pH
RCF = regional contamination factor
pHmod = pH predicted by model based on "map parameters"

substances and a high production would mean a high sedimentation and, hence, a higher resuspension of sedimentated matter.

It is evident, and it has been demonstrated (Preisendorfer 1986), that the conditions in the catchment area, such as the areal distribution of bedrocks and soils, the land use, as well as the morphometry of lakes (Håkanson and Peters 1995), such as area, volume, mean depth, etc., influence the conditions in the lake, the chemical conditions as well as the biological conditions. It is not meaningful to apply predictive models based on map parameters for site-specific data for singular events. Predictive models based on such map parameters (x) for lake chemical and biological variables (y) can only yield mean values for entire lakes for longer periods of time.

The results presented here are valid for mean Secchi depth from 36 months (Sec36 in metres). Table 4 first gives results for Sec36 versus map parameters, then for Sec36 versus state variables. One can note that the r^2-value for the model based on map parameters after four steps ($F = 4$) is as high as 0.68. The model is based on:

(*i*) D_m, a powerful predictor ($r^2 = 0.46$) that describes the fact that lake internal processes (resuspension, internal loading, etc.) affect Secchi depth very much. The larger the mean depth the larger the Secchi depth (see also Fig. 3B, which gives the regression for absolute, not logarithmic, values of mean depth vs. Secchi depth).

(*ii*) the ratio area/ADA, which shows a positive correlation; this is logical as large lakes with small catchments generally have clear waters.

(*iii*) Rock%, which has a logical positive relationship to Secchi depth. If Rock% increases, then the catchments have more infertile areas from which the transport of coloured substances, suspended inorganic materials, and nutrients would be small. The percentage of rocks in the catchment belongs to a cluster including Till% (Håkanson and Peters 1995), and it is difficult to give clear-cut causal explanation why and how this parameter enters at this particular step in the regression.

(*iv*) Lake%, which has a logical positive r-value; the larger the percentage of upstream lakes in the catchment, the greater the possibilities for entrapment for all types of materials, the lower the load of suspended matter to the target lake, and the higher the Secchi depth.

Secchi depth can be considered as a general lake index. Table 4 also give a model based on the limnological state variables. One can note that log(Sec36) may be predicted quite accurately from $col12^{½}$ and log(totP3/12) ($r^2 = 0.80$). (totP3/12 is the mean value of total P for 3 months when the last month is month 12.) pH12 does not provide any significant improvement to this model.

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Table 4. Compilation of results from different stepwise regressions for (A) Secchi depth (Sec12) for models based on map parameters, and (B) for models based on water variables (colour and total P).

Step	Variable	r^2	Model
		Secchi depth (Sec 36) versus map parameters for 88 Swedish Lakes	
1	D_m	0.46	$\log(\text{Sec36}) = 0.154 + 0.424\log(D_m)$
2	area/ADA	0.53	$\log(\text{Sec36}) = 0.005 + 0.398\log(D_m) + 0.386(\text{area/ADA})^{0.3}$
3	Rock%	0.63	$\log(\text{Sec36}) = -0.097 + 0.333\log(D_m) + 0.533(\text{area/ADA})^{0.3} + 0.111\log(1 + \text{Rock\%})$
4	Lake%	0.68	$\log(\text{Sec36}) = 0.18 + 0.316\log(D_m) + 0.672(\text{area/ADA})^{0.3} + 0.117\log(1 + \text{Rock\%}) + 0.013(\text{Lake\%})$
		Sec36 versus state variables for 45 lakes	
1	col12	0.76	$\log(\text{Sec36}) = 0.854 - 0.052(\text{col12})^{1/3}$
2	totP3/12	0.80	$\log(\text{Sec36}) = 0.977 - 0.046(\text{col12})^{1/3} - 0.19\log(\text{totP3/12})$

Lake ecosystem index: definitions and set-up

Certainly, the complexities involved in establishing simple, practical, and meaningful ecological indices sometimes seem insurmountable. Still, the benefits of even crude environmental indices are so great that they are worth pursuing. So long as one clearly states the criteria, theories, and evidence in these complicated matters, then these components can be discussed, tested, and improved.

The first step is to establish normal values (corresponding to natural, pre-industrial, reference conditions) for the state variables. These values are predicted from empirical models valid for small glacial lakes. The empirical models to be used are those based on simple map variables without DAZ correction (i.e., Rock% and not RockN, so the empirical constants in the following equations are not the same as given in Table 2).

To calculate the normal concentration of total P in lake water, it is assumed that acidified lakes tend to have lower nutrient levels and biological productivity than lakes with natural pH, a process known as acido-oligotrophication. The normal, natural, or pre-industrial mean total P is assumed to be 5% higher than the value predicted by a regression describing totP12 in contemporary Swedish lakes (i.e., normal totP12 is that regression multiplied by a regional contamination factor of 1.05). The normal or desired mean annual total P in micrograms per litre is, therefore:

(1) totP12 = 1.05 × 10 sup{1.733 + 0.013 (OL%) – 0.006 (Rock%) - 10 sup{0.189 (log RDA) – 0.148 area sup 1/2 – 0.3 (T sup 0.1)}

$r^2 = 0.51$; $n = 66$

This model accounts for regional differences in catchment characteristics (open land% (OL%), Rock%, relief (RDA), and lake morphometry (lake area and theoretical water retention time (T)).

The model accounts for many but not all factors influencing the variability in mean annual total P. The model is intended to yield a normal value of total P that can be compared with the actual value, which reflects the influence of these other factors. The ideal ratio of actual to normal totP12 is 1 and any divergence from 1 indicates a change to the ecosystem. This ratio of actual to normal values is used as an environmental indicator and that indicator is used, among others, in the determination of the ecosystem index.

Normal values for the second state variable, the 3-yr means of lake colour (col36 in milligrams Pt per litre), are calculated from the following equation (which is also based on simple map variables and not DAZ-corrected variables).

(2) col36 = 10 sup {3.031 – 0.006 (Rock%) – 1.181 (T sup 0.1) 0.025 (Lake%) + 0.022 (Mire%) sup 0.7}

$r^2 = 0.62$; $n = 91$

There is no "regional contamination factor" (like 1.05 for totP12) in the estimation of the normal values of lake colour, because there is no good evidence that lake colour has been changed by human activity in Sweden. If and when one could quantify such an influence, it could be addressed by inserting the appropriate regional contamination factor into eq. 2.

Normal mean annual values of the third state variable, pH12, are estimated from the following regression model:

(3) pH12 = 1.15(3.882 – 0.017(Mire%) + 0.324(log(area)) + 1.589($\text{RDA}^{0.1}$) + 0.292(log(1 + OL%))

$r^2 = 0.37$; $n = 94$

In this case, I assume that anthropogenic acidification has reduced the pH of lakes in southern Sweden by about 15% so the normal pH is calculated using a regional contamination factor of 1.15.

In the following simulations, all input variables (i.e., the map parameters) are set approximately at the mean values for Swedish lakes (Håkanson and Peters 1995). Thus, the conditions in an average glacial forest lake in southern Sweden are simulated.

The index reflecting the status of fish, the fish yield ratio (FYR) is defined from the following arguments:

(*i*) Actual and normal fish yield (in milligrams wet weight per square metre per year) is first calculated from the equation given in Table 3, i.e., FYR′ = 7.1(totP), where totP is the mean annual concentration of total P. The ratio between the measured of predicted actual field yield and the predicted normal fish yield constitutes the base of this equation.

(*ii*) Lake pH will influence this ratio. This influence may be quantified in different ways. Here, the focus is on one

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species of fish, roach (*Rutilus rutilus*). The reproduction and abundance of roach is very sensitive to alterations in lake pH (Håkanson and Peters 1995). This will be described by a dimensionless moderator acting upon the FYR. The moderator is 1 when the measured or predicted actual pH is equal to the predicted normal pH. Since roach cannot reproduce at pH lower than 5, the moderator is calibrated to be zero for pH = 5 when normal pH is set to 7. This gives an amplitude value of 3.5. The moderator is

(4) Y'pH = 1 + 3.5(actual pH/normal pH – 1)

(*iii*) Lake colour will also influence the FYR. Coloured, humic organic substances can be used as a carbon sources for the primary and secondary production, and an increase in colour should increase the fish yield. This will also be quantified by means of a dimensionless moderator, which is set here to influence the FYR by a factor of two if the actual colour is three times the normal colour. That is, the amplitude value is set to 0.5. The moderator is

(5) Y'col = (1 + 0.5(actual colour/normal colour - 1)

So, the FYR is

(6) FYR = (actual totP/normal totP)Y'pH Y'col

The interpretation of the FYR is that the value is 1 for a normal lake. An index of 2 means that the fish yield is 2 times higher. It is evident that these assumptions need to be tested against reliable empirical data from many lakes. The idea here is to provide a theoretical basis for such calibrations, nothing more. The same approach will be used for the plankton biomass index and the bottom fauna biomass index.

The phytoplankton biomass ratio (PBR) is based on the quotient between the actual (from measured or predicted data) and predicted normal biomasses of phytoplankton (from Table 3), i.e., 30(actual $totP^{1.4}$)/30(normal $totP^{1.4}$). This ratio is influenced by a dimensionless moderator for pH using an amplitude value of 2, so a lower pH implies a lower phytoplankton biomass; at pH = 4 (assuming a normal pH of 7.5), the value approaches 0. This ratio will increase with lake colour (more colour, more carbon, more energy). The amplitude value is set to 0.25. This means that the biomass of phytoplankton increases 25% (a factor of 1.25) as colour increases with a factor of 2.

The bottom fauna biomass ratio (BFBR) first gives the ratio between actual and normal predicted biomasses of benthos (in milligrams wet weight per square metre; Table 3), i.e., 810(actual $totP^{0.71}$)/810(normal $totP^{0.71}$). This ratio is influenced by a dimensionless moderator for pH using an amplitude value of 3, so a lower pH implies a lower phytoplankton biomass; at pH = 5 (assuming a normal pH of 7.5), the value approaches 0. This ratio will also increase with colour. The amplitude value is set to 0.15. This means that the biomass of phytoplankton increases 15% (a factor of 1.15) as colour increases by a factor of 2.

The amplitude values describe the strength of the change in the index when the actual values of the x-variables depart from the normal values. The values are chosen to be plausible possibilities. The rationale for setting the highest amplitude values for the influence of pH for the FYR and lowest for the PBR is that fish (here roach) biomass is assumed to be the most sensitive to changing pH. These assumed values serve only to describe the methodological foundation of establishing ecosystem indices.

Any change in state variables affects the key functional groups in the ecosystem and also the ratios. Such changes would also affect other important conditions in the lakes, like the concentration of toxins in fish. Alterations in lake pH, productivity, and colour would influence the uptake of mercury by fish and the concentration of Hg in fish muscle (Lindqvist et al. 1991). Figure 5A shows that the concentration of Hg in 1-kg pike (Hgpi; in milligrams per kilogram wet weight) would decrease by a factor of 1.7 (from 0.8 to 0.48) as total P increases from ultra-oligotrophic conditions (totP = 2 $\mu g \cdot L^{-1}$) to hypertrophic conditions (totP = 500). This regression is based on data from 456 Swedish lakes. Hgpi decreases significantly with an increase in lake productivity, a case of "biological dilution." This change may be described quantitatively by a dimensionless moderator. This moderator is an algorithm accounting for the empirical knowledge of the regression in a dimensionless fashion. This moderator, YtotP, is set to 1 for totP = 32. YtotP is 0.75 for totP = 500 and 1.25 for totP = 2.

Figure 5B shows a regression between Hgpi and lake colour based on data from 969 Swedish lakes. Hgpi would increase by a factor of 2.6 (from 0.49 to 1.26) as lake colour increases from 2 to 400. This change also may be described by a dimensionless moderator, Ycol, which is set to 1 for colour = 32. Ycol is 1.45 for colour = 400 and 0.5 for colour = 2. One cause for this relationship is that mercury is partly transported to the lakes with coloured substances. This is shown in Fig. 5C, which gives the highly significant regression between reactive mercury (a fraction of total Hg; see Lindqvist et al. 1991) and lake colour. More colour gives a larger lake dose of Hg and larger Hgpi values.

That knowledge will be used in an example developing a special ratio or contamination factor for mercury (CFHg). That ratio is defined by the quotient between measured or predicted actual values of Hg in 1-kg pike (Hgpi; in milligrams per kilogram wet weight) and predicted normal values of Hgpi. The reference Hgpi values for a lake with pH = 8, totP = 32 $\mu g \cdot L^{-1}$ and colour = 32 mg $Pt \cdot L^{-1}$ is calibrated to be 0.06 (Fig. 6D):

(7) CFHg = 0.06(1 + 0.61(log(actual colour)/log(normal colour) – 1))·(1 –0.31(log(actual totP)/log(normal totP) – 1)) · (1 – 7(actual pH/normal pH – 1))

Also the CFHg value is 1 when all actual values for the state variables are equal to their normal values.

From this, one may define the LEI as

(8) LEI = (FYR + PBR + BFBR + CFHg)/4

Note that if FYR (or PBR, BFBR or CFHg) is <1, then 1/FYR, etc., is used in the model instead of FYR. Thus, the LEI value is always ≥1. LEI is never allowed to attain negative values, but any departure from 1 is always negative from an ecological point of view because it represents a departure from normal. A compilation of equations used for the LEI value is given in Table 5. This is only one way to calculate a LEI value. For

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Fig. 5. (A) The relationship between data on lake total P, log(totP), and log(Hgpi) (Hgpi is the Hg content in a 1-kg pike in milligrams per kilogram wet weight) from 458 Swedish lakes. This is a highly significant relationship ($p = 0.0036$) in spite of the low r^2 (0.02) because the number of lakes (n) is large (458). These data can be used to define a dimensionless normative moderator (YtotP) expressing the impact of total P on Hgpi. The effect of a change in total P over the observed range from 2 to 500 is to change Hgpi from 0.48 to 0.8, i.e., with a factor of 1.7. The moderator may therefore be defined as: YtotP = 1 – 0.31(log(totP)/1.5 – 1), where total P = 32 [1.5 = log(32)] is the "normative" value of total P. (B) The relationship between data on lake colour, log(col), and log(Hgpi) ($r^2 = 0.071$, $p = 0.0001$, $n = 969$). The dimensionless normative moderator (Ycol) expresses the impact of colour on Hgpi. If colour varies in the range from 2 to 400, Hgpi increases from 0.49 to 1.26, i.e., a factor of 2.6. The moderator is defined as: Ycol = 1 + 0.61(log(col)/1.5 – 1), where colour = 32 (1.5 = log(32)) is the "normative" value of lake colour. (C) Mercury is transported to lakes with coloured substances from the watershed. The relationship between a given fraction of Hg in the lake water, reactive mercury (RHg in nanograms per litre) and mean annual lake colour (log(col12)) is highly significant ($r^2 = 0.55$, $p = 0.0001$, $n = 25$).

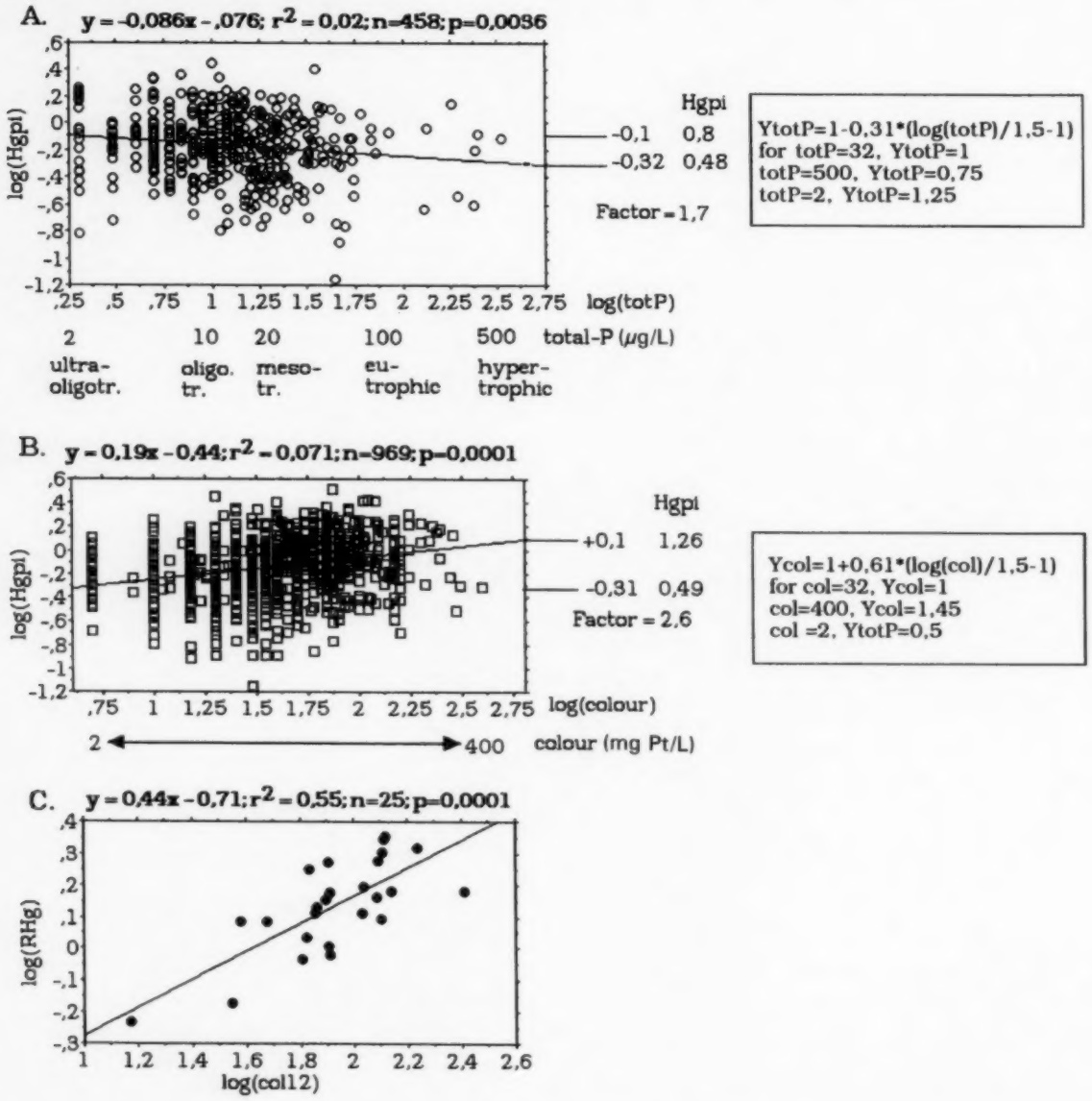

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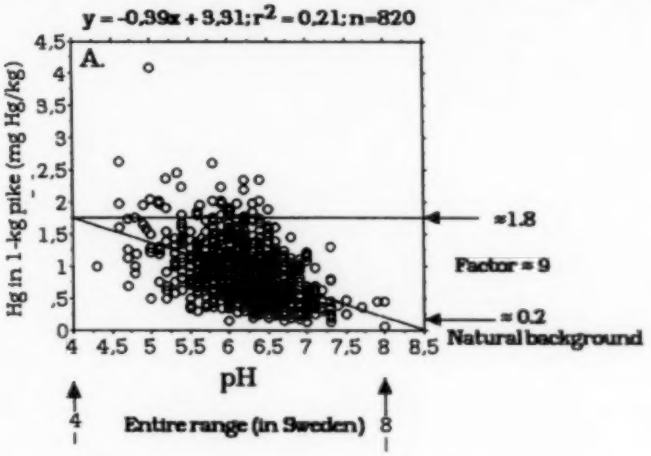
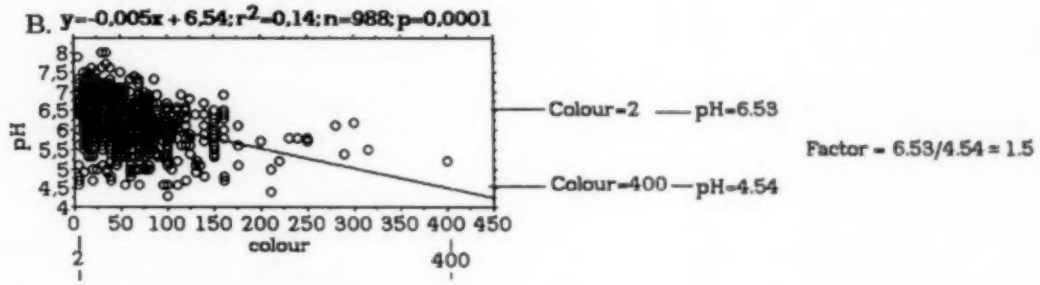
Fig. 6. (A) The relationship between scattered data on lake pH and Hgpi (Hg content in 1-kg pike) from 820 Swedish lakes from the period 1981–1986. These data can be used to define a dimensionless borderline moderator (YpH) expressing the impact of pH on Hgpi. The effect of a change in pH over the observed range from 8 to 4 is to change Hgpi ninefold from 0.2 to 1.8. Therefore, the moderator may be defined as YpH = 1 – 16(pHemp/8 – 1). (B) Coloured, humic substances are acidic, and the relationship between pH and lake colour is highly significant ($r^2 = 0.14$, $p = 0.0001$, $n = 988$). If colour varies in the range from 2 to 400, pH would, on average, decrease from 6.53 to 4.54, i.e., with a factor of 1.5. (C) The burning of fossil fuels leads to emissions of sulphur, nitrogen, and many metals, like mercury. Thus, a decrease in pH could be causally related to an increase in precipitated Hg, and to higher Hg levels in lake fish. The initial relationship between pH and Hgpi is biased in at least two ways, firstly because there exist a relationship between pH and lake colour (a factor of 1.5), secondly because there should also exist a relationship between pH and the atmospheric load of Hg. A natural, preindustrial value of Hgpi should be better described by a pH-moderator giving not a range of 9, but about half of that, i.e., 4.5. (D) The model to predict a natural Hgpi value from the dimensionless moderators for total P (YtotP), colour (Ycol) and pH (YpH). The empirical constant 0.06 is calibrated to give a Hgpi value of 0.06 for pH = 8 (the borderline value), total P = 32 and colour = 32 (the "normative" values). This gives realistic natural Hgpi values (from 0.06 to 0.37) for different values pH, total P, and colour.



Dimensionless moderator pH vs Hgpi

Y'pH=1-16*(pH/8-1)

from pH 4 to 8, a factor of 9
for pH=8, Y'pH=1
pH=4, Y'pH=9



C. But acidification (pH) and Hg-contamination are also linked to the burning of fossil fuels, so the moderator for natural Hgpi vs pH should give a range of less than 9/1.5, or about 9/2:

YpH=1-7*(pH/8-1)

for pH=8, YpH=1
for pH= 4, YpH=4.5. The range is 4.5

D. Model:
Hgpi=0,06*YtotP*Ycol*YpH

pH	totP	col	Hgpi
8	32	32	0.06
7	10	100	0.15
6	5	200	0.25
5	3	300	0.37

example, one could also use log values instead of the absolute values of the ratios in defining LEI, and different weighing functions could be applied to stress that, for example, the fish biomass ratio is so important that $FYR^{1.4}$ should be used and not FYR[1] and that the special index for Hg is "only" an operational tool for management that informs very little about the state of the ecosystem so $CFHg^{0.6}$ should be used instead of CFHg[1].

This approach holds potential for lake management, as will now be demonstrated. Assume that in the average, "normal"

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Table 5. A compilation of equations used for the lake ecosystem index.

1. Fish yield ratio (FYR) = (actual fish yield/normal fish yield) × Y'pH × Y'col
Fish yield = 7.1(totP) (in mg ww·m^{-2}·yr^{-1})
Moderator for pH (Y'pH) = 1 + 3.5(actual pH/normal pH – 1)
Moderator for colour (Y'col) = 1 + 0.5(actual colour/normal colour –1)
2. Phytoplankton biomass ratio (PBR) = (actual biomass/normal biomass) × Y''pH × Y''col
Phytoplankton biomass = 30(totP)$^{1.4}$ (in mg ww·m^{-3})
Y''pH = 1 + 2(actual pH/normal pH – 1)
Y''col = 1 + 0.25(actual colour/normal colour – 1)
3. Bottom fauna biomass ratio (BFBR) = (actual biomass/normal biomass) × Y'''pH × Y'''col
Bottom fauna biomass = 810(totP)$^{0.71}$ (in mg ww·m^{-2})
Y'''pH = 1 + 3(actual pH/normal pH – 1)
Y'''col = 1 + 0.15(actual colour/normal colour –1)
4. Contamination factor for mercury (CFHg) = YtotP × Ycol × YpH × 0.06
5. Lake ecosystem index (LEI) = (FYR + BFBR + PBR + CFHg)/4

Note: If FYR (or BFBR, PBR, and CFHg) < 1, then use 1/FYR instead of FYR.
Thus, LEI is always ≥1. A departure from LEI = 1 is always negative.

lake, the mean annual total P is 10.3 μg·L^{-1} (i.e., an oligo-mesotrophic lake), mean 3-yr colour is 78.5 mg Pt·L^{-1} (i.e., a rather humic lake) and normal annual mean pH is 7.0 (i.e., a lake with neutral water). Figure 7A1 illustrates the simulated changes in the lake ecosystem index and Fig. 7A2 the corresponding changes for the four ratios under the influence of acidification over the last 40 yr, as given by the actual values of mean annual pH (curve 1; the driving function). For this simulation, the actual total P and lake colour were constant at their defined normal values. The natural or reference value for the LEI is 1 when lake pH is normal (pH = 7.0), and a LEI value of 2 implies that the original, normal biomasses of the lake ecosystem (and the Hgpi concentration) on average have been doubled (i.e., a 100% departure from the normal). This is a very significant alteration of the entire lake ecosystem. From Fig. 7A2, one can note that all biomasses decrease during the simulated period of acidification, but the Hgpi values increase.

Figure 7B gives a sensitivity test where lake colour is constant at 78.5 and pH constant at 7. The figure gives simulated effects on LEI and the four ratios of variations in lake total P. The normal value for lake total P is set to 10.3. Figure 7B2 shows that all biomasses vary with the values of total P, and that the contamination factor for mercury decrease when total P increase (a case of biological dilution).

These simulations demonstrate how variabilities in the state variables influence the lake ecosystem index: very high values of LEI can be obtained if the actual values of all three state variables depart significantly from the normal values. These simulations indicate that the approach has potential in limnology and water management because it would facilitate overview and provide an aim and direction for remediation. However, LEIs will not be of practical use until the models have been calibrated and validated against reliable, empirical data from many lakes.

Regional modelling from a GIS platform

Ideally, environmental indices and operational variables should express important relationships and be comprehensible without expert knowledge. In fact, one reason to develop environmental indices is so that politicians and the public can understand the present condition and future changes in the environment.

Environmental indices have the advantage of expressing the environmental status simply, but they simultaneously pose problems in that a great deal of information is lost in aggregating the individual measures. This disadvantage is reduced if one knows what an index represents, and if one can access the individual components. An aggregated index of environmental health could complement the picture of the country's economic development given by the GNP. An environmental state index could be compared with a consumer price index.

How, then, should the status of such an ecosystem be described in practice? The first problem is that each ecosystem type, e.g., fresh waters, is not a uniform entity. If one starts with the threat to fresh waters, it is clear that, for example, eutrophication and toxic contamination threaten fresh waters and that these threats might be manifest in reduced biological diversity and contaminated fish. One way of relating the threat to the possible effects is illustrated in Fig. 8. Cadmium is used as an example, but the basic principles apply to other chemical threats as well. Cadmium is not a major threat to freshwater plants and animals, but studies (mainly in the laboratory) show (see Håkanson and Jansson 1993) that certain species are sensitive to cadmium and that others are not (Fig. 8A). In the case of the most sensitive species, cadmium concentrations in water of 0.1-10 μg·L^{-1} disturb reproduction. If these sensitive species are key functional groups and cannot be replaced by other related species, then cadmium concentrations as low as 0.1-10 μg·L^{-1} will affect the ecosystem. The target organisms (Fig. 8) are the most sensitive, important species in the ecosystem, but their roles may be critical in only some fresh water ecosystems, e.g., in oligotrophic lakes. Such lakes are then the target ecosystems for this effect. This example illustrates the environmental sensitivity: one and the same load (= dose) may cause different environmental effects in ecosystems with different sensitivity. Consequently, it is important to define both target organisms and target ecosystems for a given threat (CGLRM 1991).

Figure 9 illustrates the practical use of a regional ecosystem index for fresh waters. Index values could be obtained for each county and the development within regions could be illustrated

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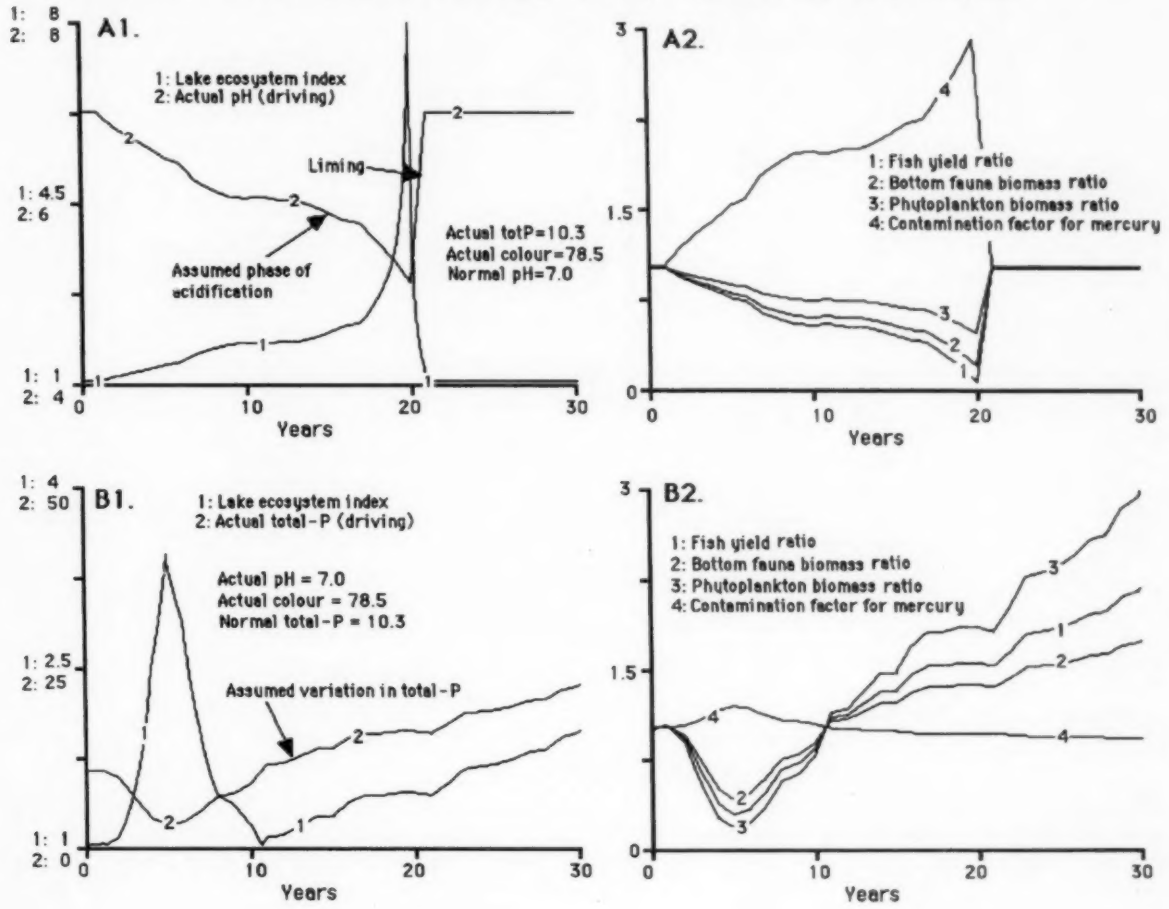
Fig. 7. Simulations and sensitivity tests with the model for the lake ecosystem index. The normal values for the three state variables are total P = 10.3 $\mu g \cdot L^{-1}$, colour = 8.5 mg $Pt \cdot L^{-1}$, and pH = 7. (A) Sensitivity analyses illustrating the influence of acidification (curve 2 in Fig. A1; pH is the driving variable in all tests illustrates in Figs. A1 and A2) on the lake ecosystem index (curve 1 in Fig. A1), and the corresponding curves for the fish yield ratio, the bottom fauna biomass ratio, the phytoplankton biomass ratio and the contamination factor for mercury (in Fig. A2), while colour and total P remain normal. (B) Sensitivity analyses to illustrate how assumed changes in lake total P (eutrophication) influence the lake ecosystem index and the four ratios, when pH and colour are held at their normal values.



with trend analyses. If these trends were linked to remedial measures, the effect of the remedies could be discussed qualitatively and quantitatively. Presentations like this use GIS together with regional models based on map parameters.

In practice, any LEI is determined for a limited number of lakes. The information is, therefore, lake typical. To get region-typical information, which ought to have high priority with environmental authorities, one must integrate or sum these lake-typical values of LEI over area and time to achieve a total lake ecosystem index (TLEI), which is simply the sum (or the average or some other defined function) of the LEI values for a given region.

Environmental cost-benefit analyses

The following section will present an outline of an environmental cost-benefit analysis (Fig. 10). The goal of the analysis is to quantify what one gets for the money. The example assesses four different remedies: lake liming, liming plus fertilizer, liming plus potassium treatment, and wetland liming (see Håkanson et al. 1990; Håkanson 1992). The price for the remedial measures varies from a mean value of 295 000 Swedish kronor (SEK)·km^{-2} for the least expensive remedy, lake liming, to 1.27 million SEK·km^{-2} for the most expensive, lake liming plus potassium treatment. An effect of remediation can be determined quite simply. For example, the state variable, pH, increases following liming (dpH). However, the remedial measures influence the entire lake ecosystem and it is more difficult to measure the effect of the remedy on all of the lake's biology. Here, the change in LEI is used as a holistic measure of the ecosystem's response to remediation.

The change in the lake ecosystem index (dLEI) is illustrated

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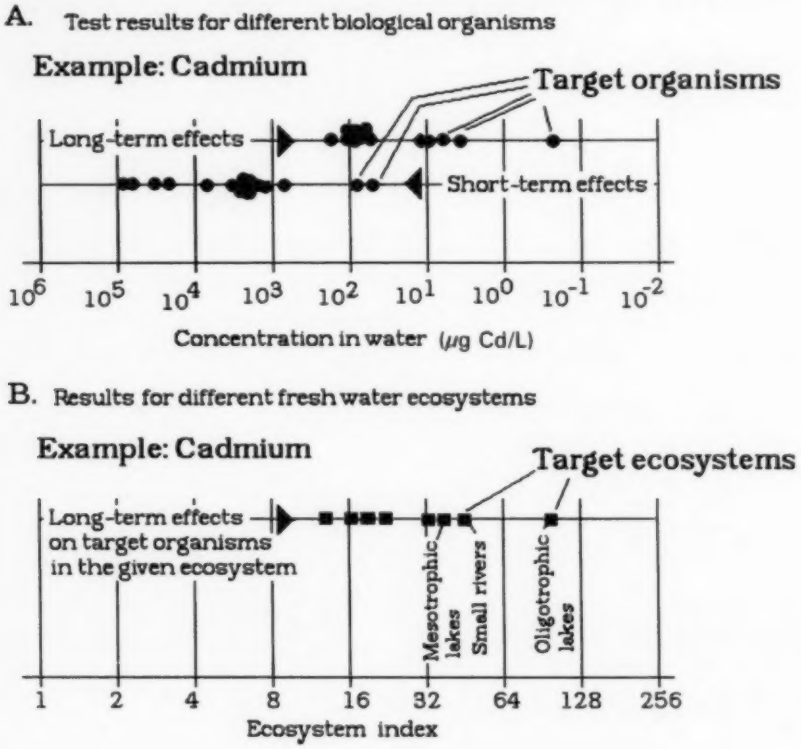
Fig. 8. (A) Illustration of target organisms. Data on environmental effects of cadmium in short- and long-term laboratory tests (SNV 1980; Håkanson and Jansson 1983). The most sensitive organisms in long-term tests are the most appropriate target organisms. The tests may indicate the weakest link in the eco-chain and the concentration at which that link breaks, but they do not show that this organism is critical to ecosystem function. (B) An illustration of the identification of (hypothetical) target ecosystem types according to their sensitivity to Cd, where this sensitivity is the sum of proportional changes in a series of key functional groups represented as an ecosystem index.


A. Test results for different biological organisms
Example: Cadmium
Target organisms
Long-term effects
Short-term effects
10^6 10^5 10^4 10^3 10^2 10^1 10^0 10^-1 10^-2
Concentration in water (μg Cd/L)
B. Results for different fresh water ecosystems
Example: Cadmium
Target ecosystems
Long-term effects on target organisms in the given ecosystem
Mesotrophic lakes
Small rivers
Oligotrophic lakes
1 2 4 8 16 32 64 128 256
Ecosystem index

in the table in Fig. 10 and in the three-dimensional diagram where it is linked to the annual mean total P concentration and the annual mean pH of the lake. Thus, dLEI considers the influence of liming on the planktonic, benthic, and fish biomasses, as well as the CFHg. The influence of fertilization may be positive in extremely oligotrophic lakes but negative in more productive waters. If one regards the costs of the remedies and the ecological consequences in the table in Fig. 10, one can see that an expensive measure (wetland liming) has the best cost/benefit ratio (0.4) whereas less expensive measures (e.g., lake liming) give lower ratios. From an ecosystem perspective, wetland liming is preferable.

Once the costs of remediation are known, it is possible to calculate the cost of returning the LEI to a value of 1; the state that was defined as normal by the index. This approach defines the environmental cost-benefit analysis in terms of the environmental effects rather than in terms of dose variables. The latter would be much easier, but they are much less interesting and informative.

Figure 11 highlights the links among the ecosystem index, remediation costs, and a "green GNP." It shows that it may be possible to set a price on the damage to the environment, if one accepts the price is the cost of restoring the system to its normal values. The *y*-axis in Fig. 10 gives the LEI per unit area (here square kilometres) and time (here 1 yr) for different (hypothetical) situations where the remedial costs have been related to the changes in the ecosystem indices. The four more realistic examples for lakes from Fig. 10 are marked. Logarithmic scales are used because remediation is likely more costly at later stages of environmental deterioration than at early ones. If mean values of the ecosystem indices (for lakes, coasts, forests, natural land, agricultural land, and urban areas) for defined regions are multiplied by the corresponding areas of those ecosystems (see Table 6), then that product could be used to complement the traditional GNP, demonstrating the environmental costs of development. The total costs of all damage to the six ecosystems in the region (a small commune of 560 km^2) in Table 6 amount to 20 200 million SEK. The benefits of this approach would be even more evident if this analysis were applied to entire countries with maps like Fig. 9 (presumably using GIS methodologies). This would mean that the GNP would not account just for the annual production value of goods and services, but also include a monetary value expressing the status of the environment, as the "ecological debt," and the change in this value each year could be treated as the annual ecological deficit.

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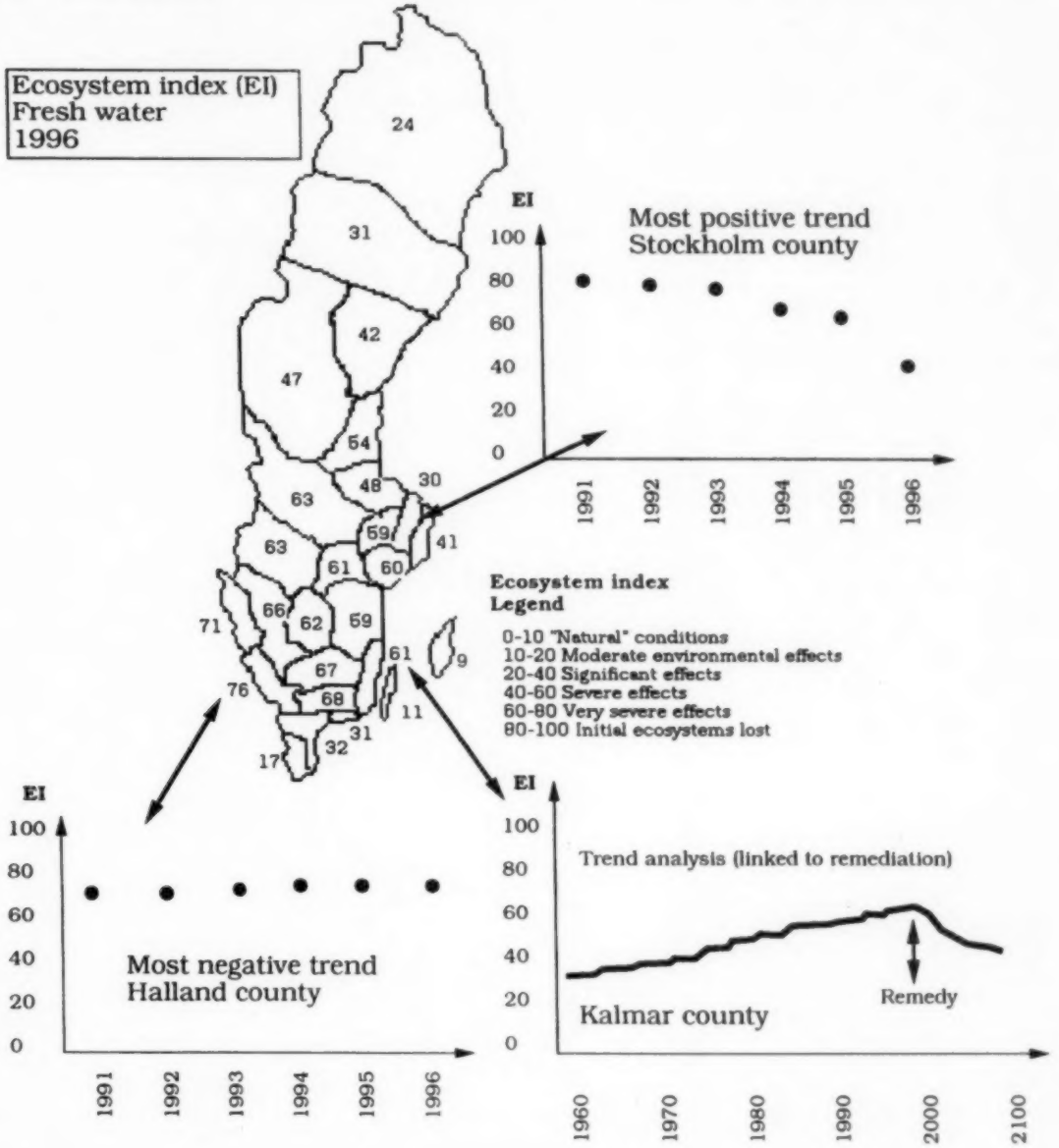
Fig. 9. An example of the ecosystem index for fresh water showing a map of Sweden illustrating (hypothetical) values for Sweden's 24 counties in 1996, a trend analysis for the county with the greatest improvement (Stockholm), a trend analysis from Halland, the county with the most deterioration, a long-term analysis showing the effect of remedial measures in the county of Kalmar, and a legend for the data classes. From Håkanson (1993*a*).



This approach would mean that it would be possible to create a scientific link between economy and ecology. For example, the burning of fossil fuels can be visualized and quantified in terms of production of oil, petrol, etc., and by many different financial flows (incomes, taxes, revenues, etc.). This information is currently summarized in the GNP. On the other hand, the burning of fossil fuels also means destruction of a portion of the nonrenewable fossil capital of this planet, and it leads to severe ecological damage in terms of acidification, contamination, eutrophication, health problems, etc. The green GNP or ecological debt would allow comparison of these costs with the traditional economic indicators.

Concluding remarks

(*i*) If the aim is to quantify, rank, predict, and simulate,

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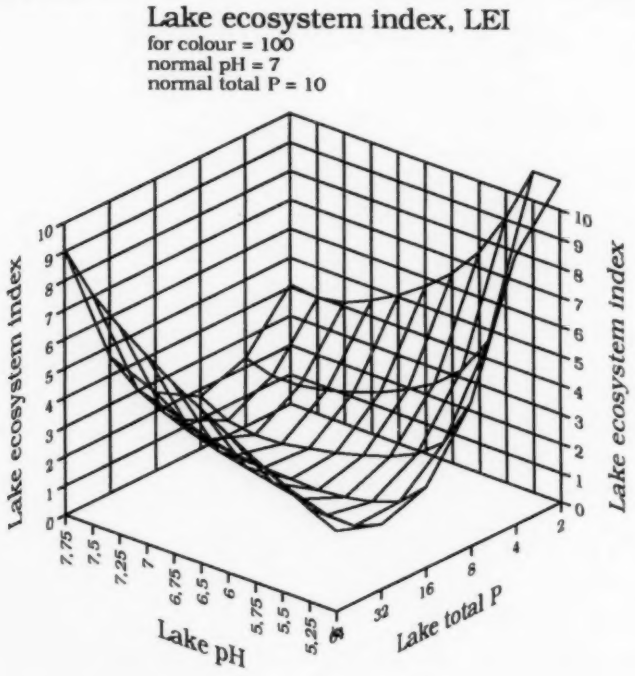
Fig. 10. Illustration of an environmental cost-benefit analysis. (Upper) Table of four different remedial measures that are tested in this hypothetical example for a lake ecosystem. All the given measures (lake liming, wet land liming, and fertilization) will influence the lake ecosystem. Here, these extremely complicated interactions have been quantified by, first, two simple state variables, lake water pH (dpH means change in mean annual lake pH due to remediation) and total P (dP) and by a Lake Ecosystem Index (LEI), which includes mercury in lake fish. The cost/benefit number (CB) expresses the relationships between the costs (in the first column) for these four remedies in relation to the environmental benefits, as determined by the duration of the remedies, the size of the areas affected by the remedies and the change in the LEI values; the higher the CB the more environmental improvements one gets for the money invested in these measures. (Lower) Three-dimensional figure showing LEI as a function of pH and total P. A change in pH and (or) total P could have both positive and negative for the target organisms used to determine the LEI value. In this particular model, LEI is 1 (i.e., the reference, normal condition) when pH = 7, total P = 10 $\mu g \cdot L^{-1}$ and colour = 100 mg $Pt \cdot L^{-1}$. Any departure in pH and total P from these values would increase the LEI value.

Example: Cost-benefit analysis using the Lake Ecosystem Index
(This is calculated for a lake with initial values of pH12=5.5 and totP12=4.9.)

				Change in state variables		Change in LEI	
A. Remedial measure	Costs/volume (10^3 SEK/km^2)	Duration (T, years)	Affected area (A, km^2)	dpH12 (units)	dtotP12 (μg/L)	dLEI (index)	**CB-number=** (dLEI*T*A/SEK)
Lake liming	**295**	**3**	**5**	0,8	2	**2,95**	**0,2**
Lake liming+fert.	**695**	**3**	**5**	1	5	**3,6**	**0,1**
Lake liming+potash	**1270**	**5**	**5**	0,9	3	**3,25**	**0,1**
Wet land liming	**987**	**10**	**10**	1,2	6	**3,8**	**0,4**
Range of variables in Swedish glacial lakes				(4-7.5)	(4-50)		
Is change positive or negative?		(+)	(+)	(+)	(+)	(+)	



few, if any, alternatives exist to models in complex ecosystems. "Verbal models," "qualitative explanations," and "logical reasoning" often deteriorate into "environmental theology," rather than environmental science.

(*ii*) Dynamic models are logical constructs. But logical

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Fig. 11. A hypothetical relationship between different ecosystem state indices from different types of ecosystems (urban, forest, coastal, and freshwater ecosystems) and costs related to remedial measure affecting the ecosystem indices. It represents a quantitative relationship between economy and ecology.

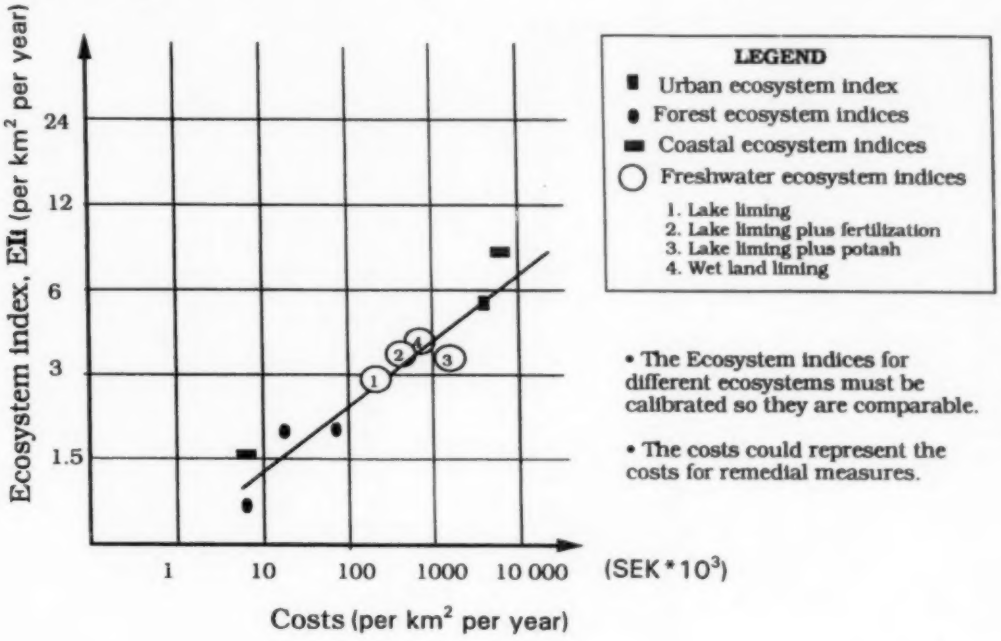

Table 6. Illustration of how to link ecosystem indices to remedial costs quantitatively for a hypothetical region (e.g., a country, province, county or commune).

Ecosystem	Mean ecosystem index (EI) (EI·km^{-2}·yr^{-1})	Area (km^2)	Total EI (EI × area)	Remedial costs (million SEK·km^{-2}·yr^{-1})	Total costs (million SEK)
Fresh waters	3	20	60	40	800
Coastal areas	2	30	60	10	300
Forests	4	100	400	100	10 000
Natural land	2	150	300	10	1 500
Agricult. land	2.5	250	625	30	7 500
Urban areas	2	10	20	10	100
Sum	15.5	560		200	20 200
Mean	2.58				

reasoning depends on personal knowledge and some of that knowledge may be subjective. What is logical for one person may be illogical for another. Logic in ecology is not objective, but subjective; it is in the mind of the beholder.

(*iii*) Big models are often "prescriptive" not predictive. Big models may look more objective than small, but this may be self-deception.

(*iv*) Models are built and validated with empirical data. Empiricism enters at many steps from start to finish in modelling. But empirical data, and any knowledge based on empirical data, are uncertain. Accumulated uncertainties in the models will cause accumulated uncertainties in model predictions.

(*v*) The predictive power of a model is not governed by the strength of the model's strongest part, but by the weakness of its weakest part.

(*vi*) Big models are simple to build, but hard to validate. Small models are hard to build, and simple to validate.

(*vii*) Small size is necessary, but not sufficient, for utility and predictive power, so useful models must be small. Small models should be based on the most fundamental processes, but that is far easier to say than it is to accomplish.

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(*viii*) Scientific knowledge does not lie in the model alone, nor in the empirical data alone, but in their integration as validated, predictive models.

(*ix*) The key issue is not to verify, but to falsify a model, and thereby to determine its limitations.

(*x*) It is important to predict mean values, but it is equally important to predict the confidence interval around the mean.

(*xi*) When using models for ecosystems (for entire lakes, coastal areas, etc.), it is not possible to describe phenomena at the individual, organ, or cell levels.

(*xii*) The drawback of empirical models is their restricted range of application, and, although empirical models should be based on time- and area-compatible *x*- and *y*-variables, they generally do not describe time-dependent processes, like seasonal variations.

(*xiii*) All model approaches have drawbacks and limitations. In dynamic models, scientific knowledge is used to set the processes, but guesses are used to set the rates. In empirical regression models, science is used to get the constants and guesses are made about the processes. Both approaches have their places. But the predictive power lies in the choice of the constants and model variables, rather than in discussions about the most logical processes. Dynamic models are basic tools to address problems related to fluxes of material, like carbon or pollutants, amounts and concentrations in water, sediments and biota, but not effects on the ecosystem level.

(*xiv*) One interesting avenue for future research is the application of different types of GIS in predictive modelling.

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Linking fish habitat to their population dynamics

Daniel B. Hayes, C. Paola Ferreri, and William W. Taylor

Abstract: We classify habitat features based on their effects on fish population dynamics and how fish populations affect the habitat's dynamics. We term habitat features that can be reduced in quantity or quality by fish usage as consumable resources. In general, consumable resources regulate fish populations in a density-dependent manner. In contrast, nonconsumable habitat features influence fish populations in a density-independent manner. We further classify habitat features by the influence that fish have on the supply of that resource. We designate habitat features whose supply is unaffected by fish usage (e.g., space) as being dynamically unaffected. Thus, the supply of these resources does not depend on the present or past abundance of fish. The supply of dynamically affected habitat resources (e.g., prey abundance) depends on current and past fish abundance. Using lake whitefish (*Coregonus clupeaformis*), we illustrate how changes in fish habitat can be integrated with changes in fish growth, survival, and reproduction through a stock–recruitment relationship. This example shows that single measures of population response such as carrying capacity or changes in surplus production do not fully represent the population-level changes following a habitat alteration.

Résumé : Nous classons les caractéristiques de l'habitat en fonction de leurs effets sur la dynamique des populations et de la façon dont les populations de poisson influent sur la dynamique de l'habitat. Nous qualifions de ressources consommables les caractéristiques de l'habitat qui peuvent subir une réduction quantitative ou qualitative suite à leur utilisation par le poisson. De façon générale, les ressources consommables exercent un effet régulateur sur les populations de poisson qui est fonction de la densité. Au contraire, les caractéristiques de l'habitat non consommables influent sur les populations d'une façon indépendante de la densité. Nous classons aussi les caractéristiques de l'habitat en fonction de l'influence des poissons sur l'approvisionnement de la ressource. Nous désignons comme dynamiquement stables les caractéristiques de l'habitat dont l'approvisionnement n'est pas affecté par l'utilisation qu'en font les poissons (espace, etc.). L'approvisionnement en ces ressources n'est donc pas fonction de l'abondance actuelle ou passée du poisson. L'approvisionnement des ressources de l'habitat régulées de façon dynamique (abondance des proies, etc.) est fonction de l'abondance actuelle ou passée du poisson. Nous illustrons, en prenant comme exemple le Grand corégone (*Coregonus clupeaformis*), la façon dont les modifications de l'habitat du poisson peuvent être intégrées aux modifications de la croissance, de la survie et de la reproduction des poissons par le moyen d'une relation stock-recrutement. Cet exemple montre que des mesures uniques de la réponse d'une population, comme la capacité limite ou la production excédentaire, ne reflètent pas complètement les modifications de niveau de population découlant d'une perturbation de l'habitat.
[Traduit par la Rédaction]

Introduction

This paper outlines several ways that fish population dynamics are linked to their habitat. Specifying these linkages provides the conceptual basis for habitat-based fish population models that are needed by fishery managers and researchers to predict the effects of habitat changes on fish populations. Before doing this, it is useful to examine how fish habitat has been defined, and consider how habitat and population dynamics are associated under these definitions. A common paradigm of fish habitat focuses on the physical and chemical characteristics of the environment, explicitly excluding biological factors as part of "habitat." For example,

> "Habitat for fish is a place—or for migratory fishes, a set of places—in which a fish, a fish population or a fish assemblage can find the physical and chemical features needed for life, such as suitable water quality, migration routes, spawning grounds, feeding sites, resting sites, and shelter from enemies and adverse weather. Although food, predators, and competitors *are not* habitat, proper places in which to seek food, escape predators, and contend with competitors *are* part of habitat, and a suitable ecosystem for fish includes habitat for these other organisms, as well" (Orth and White 1993).

An advantage of this definition is that fishery managers and researchers can quantify and compare habitat at different locations and times relatively easily because physical and chemical characteristics of the environment are often readily measured. However, it is difficult to directly link fish population dynamics to habitat using definitions based solely on physical and chemical environmental characteristics because the growth, survival, and birth rate of fish also depend on the biotic characteristics of their environment. For example, the survival of young fish may be greatly enhanced by cover (e.g., aquatic macrophytes) if predatory fish are abundant, but the value of macrophytes is less if predatory fish are scarce (e.g., Werner

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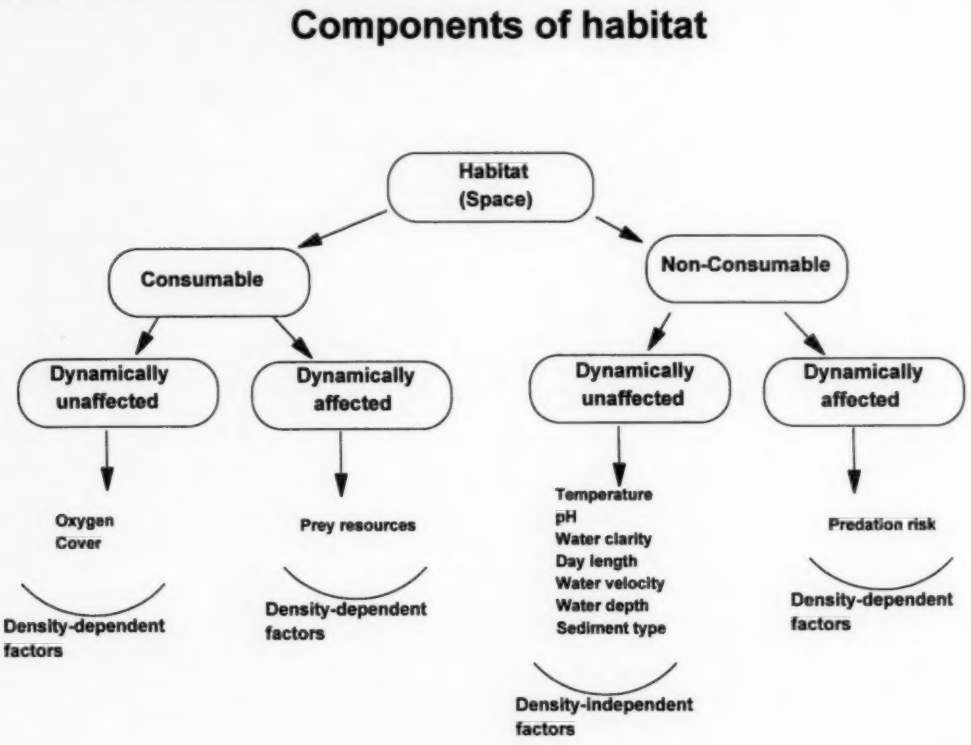
Fig. 1. A classification scheme for components of fish habitat based on whether they can be consumed by fish and whether fish affect the processes (i.e., the dynamics) generating the habitat component.



et al. 1983; Werner and Hall 1988; Tabor and Wurtsbaugh 1991).

Because biotic and abiotic factors play an important role in determining fish growth and survival, a definition of habitat that includes both biotic and abiotic components of the environment is essential to construct models relating habitat quality and quantity to fish population dynamics. The definition of habitat we prefer is the following:

> "Habitat is simply the place where an organism lives.... Physical, chemical and biological variables (the environment) define the place where an organism lives. Niche, a closely related term defines the way a species adjusts to other related species in this space." (Hudson et al. 1992).

In this definition, space is the primary component of fish habitat, and other resources and environmental conditions modify the utility of space. A difficulty in using such a broad view of fish habitat is that different components of the environment affect fish populations in different ways. To help put the different components of fish habitat into a framework useful for linking habitat variables to fish population dynamics, we propose a scheme for categorizing different environmental (habitat) characteristics based on how they regulate fish populations and how fish usage affects the habitat itself.

Classifying habitat characteristics

The first criterion we use in classifying habitat characteristics or components is whether they are consumable or nonconsumable (Fig. 1). We define consumable habitat components (resources) as features of the environment that can be depleted by fish usage (Tilman 1982). Consumable habitat components include biotic (e.g., prey resources) and abiotic (e.g., oxygen and cover) resources (Fig. 1). In contrast, nonconsumable habitat features can be thought of as environmental conditions that are not depleted by fish usage. Most nonconsumable elements of habitat are physical or chemical in nature; these include variables such as temperature, pH, day length, and water depth (Fig. 1). Predation risk, however, is a biological variable that we also categorize as nonconsumable. Like temperature, predation risk is a habitat component that is not "consumed."

The distinction between consumable and nonconsumable types of resources is important because they differ in how they affect fish population dynamics. In general, consumable resources can control fish populations through density-dependent regulation (e.g., Pielou 1974; Tilman 1982). This occurs because the amount of these resources available per fish declines with fish abundance. For example, the amount of space for a fish's territory depends upon the space used by other fish for their territories. Thus, with increasing fish density, space becomes more limiting, resulting in lower growth and (or) survival (e.g., Grant and Kramer 1990). Nonconsumable envi-

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Fig. 2. Features of stock–recruitment curves.

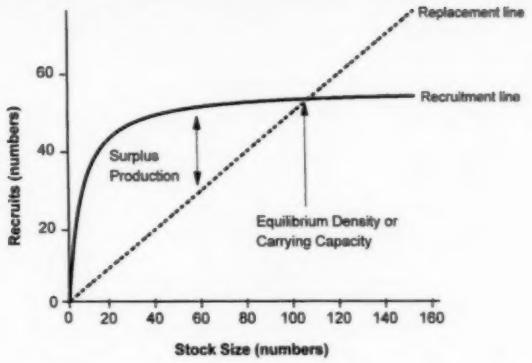
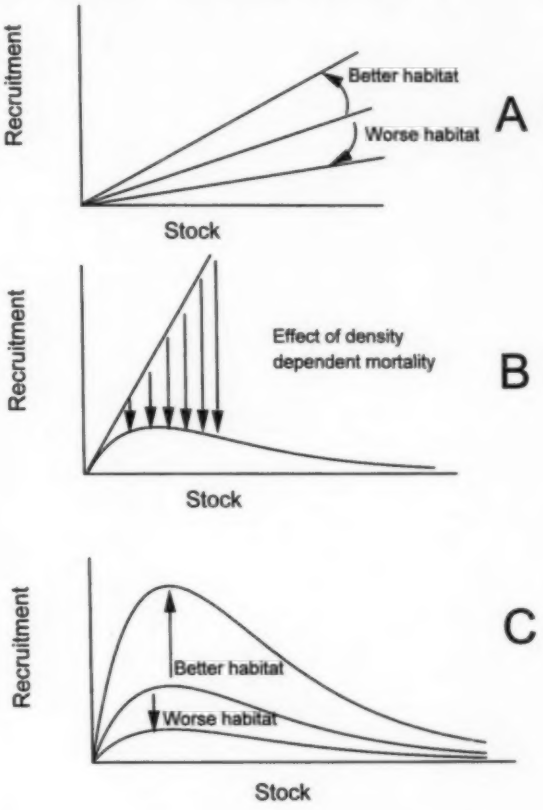


Fig. 3. Linkage between habitat conditions and recruitment. (A) Changes in recruitment when nonconsumable, dynamically unaffected habitat components (i.e., density-independent factors) are altered. (B) Effect of density-dependent mortality (i.e., limitation by consumable or dynamically affected habitat components) on recruitment. (C) Changes in recruitment for different habitat conditions when recruitment is governed by both density-dependent and density-independent factors.



ronmental conditions generally cause density-independent fluctuations in birth and death rates (Fig. 1) because these "resources" are not depleted with increasing fish density (Tilman 1982). Nonconsumable habitat conditions are typically associated with space or cover and as such may regulate fish populations in a density-dependent manner (e.g., Pielou 1974). The importance of the association between environmental attributes and space is that virtually all limiting factors may appear to operate in a density-dependent manner since space itself is a consumable resource. For example, temperature itself is a nonconsumable resource, but places (i.e., space) with appropriate or optimal temperatures are a consumable resource.

The next classification criterion we propose is whether the supply of the habitat variable itself is affected by fish usage or not (Fig. 1). For example, the "supply" of temperatures in a river or lake is unaffected by fish "usage." That is to say that the temperature regime in a river or lake is unaffected by the presence or absence of fish. We term these habitat components as being dynamically unaffected (Fig. 1). Note that dynamically unaffected habitat components are not necessarily static or stable habitat features; we use the term dynamically unaffected only to indicate that the processes generating changes in these components over time and space are unrelated to the abundance of fish. In contrast, an example of a dynamically affected habitat component is prey resources. Fish consumption affects the dynamics of their prey resources by altering the abundance, production, and size structure of prey resources over time (e.g., Brooks and Dodson 1965). As such, we term these habitat features as being dynamically affected.

As with consumable resources, dynamically affected habitat components limit fish populations through density dependence (Fig. 1). A particular example of this is the regulation of fish populations through predation. While predation risk is a nonconsumable feature of fish habitats, the abundance and behavior of predators can be influenced by the density of their prey species (e.g., Werner et al. 1983). Dynamically unaffected habitat characteristics can operate in a density-dependent (e.g., space) or density-independent manner (e.g., pH), depending upon whether they are consumable resources or nonconsumable environmental conditions (e.g., Pielou 1974).

Linking habitat variables to population dynamics

The rate of increase or decrease of a population depends on the net difference between birth rate and mortality rate at a given population size. The trajectory of a population over time, however, depends on how these rates vary as a function of population size and density-independent factors. Because of the central role that the birth and death processes play in fish population dynamics, our analysis will focus on how changes in habitat variables affect these rates.

One way of depicting the dynamics of a fish population that encapsulates birth and death rates in the context of density dependence is through a stock–recruitment relationship (e.g., Ricker 1954; Beverton and Holt 1957). In a stock–recruitment relationship, the birth rate is characterized by the number of recruits entering the population annually (recruitment line; Fig. 2). If the survival of recruits is density inde-

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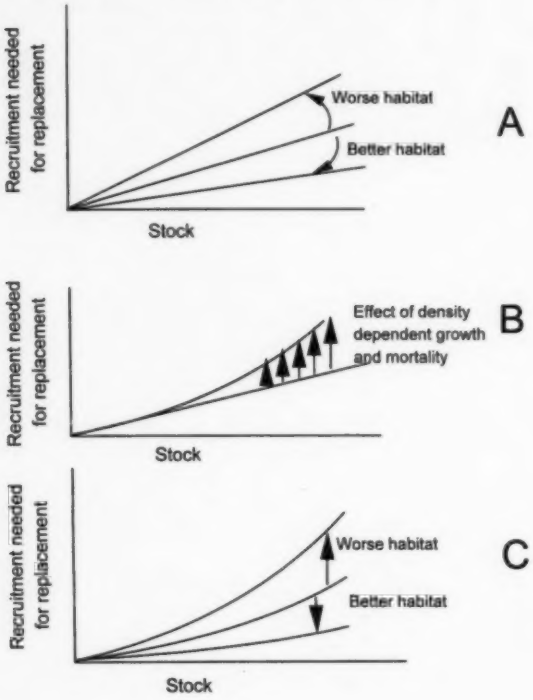
Fig. 4. Linkage between habitat conditions and the replacement line. (A) Changes in the replacement line when nonconsumable, dynamically unaffected habitat components (i.e., density-independent factors) control adult growth and survival for different habitat conditions. (B) Effect of density-dependent mortality (i.e., limitation by consumable or dynamically unaffected habitat components) on replacement line. (C) Changes in the replacement line for different habitat conditions when adult growth and survival are governed by both density-dependent and density-independent factors.



pendent, stock (measured by egg production or spawning stock biomass) and recruitment are related by the equation: $R = aE$, where R is recruitment, E is egg production, and a is survival rate of young. This produces a linear relationship between stock and recruitment (Fig. 3A), and implies that nonconsumable, dynamically unaffected habitat components are limiting the survival of young fish. In this situation, if the habitat is improved to increase the survival of recruits, the slope of the line increases. Conversely, if the habitat is degraded, the number of recruits produced at a given level of stock is reduced.

The effect of density-dependent mortality is to decrease survival relative to the density-independent recruitment line (Fig. 3B). The shape of the resulting recruitment line depends upon the rate at which mortality increases with stock size (Shepherd 1982). As with the density-independent case, improvements in habitat result in higher recruitment for all stock sizes (Fig. 3C). As indicated earlier, density dependence occurs when consumable or dynamically affected habitat components are limiting. Some examples of habitat components that operate in a density-dependent fashion include limitations on the amount of spawning habitat or the abundance of prey resources.

In the analysis of stock and recruitment, the effect of postrecruit (adult) survival and growth are represented by the replacement line (Fig. 2; e.g., Paulik 1973; Shepherd 1982; Sissenwine and Shepherd 1987; Christensen and Goodyear 1988; Norris 1991). When survival and growth of adults are density independent, the replacement line is a straight line (Fig. 4A). When habitat is improved by reducing the limitation imposed by nonconsumable, dynamically unaffected environmental conditions, survival or growth is enhanced. This results in a shallower slope to the replacement line because fewer recruits are needed to replace the adults lost to mortality (Fig. 4A). As with the recruitment line, departures from linearity in the replacement line result from density-dependent control of growth and survival rates (Figs. 4B and 4C). Density-dependent habitat limitation may occur in a number of ways during the postrecruit stage of life through the action of consumable or dynamically affected habitat components. Some examples include increased adult mortality because of the limited amount of space available for territories at high stock sizes (e.g., Grant and Kramer 1990) or decreased growth and fecundity because of food limitation at high stock sizes (Hayes and Taylor 1990).

To determine the dynamics (i.e., trajectory over time, rate of growth, and equilibrium point(s)) of the population, the recruitment and replacement lines are combined in the same graph (Fig. 2). Several features of the stock–recruitment relationship are useful for describing how populations respond to habitat alterations. The first of these features is the point (or points) where the replacement line intersects the recruitment line (Fig. 2). For unexploited populations, this intersection represents carrying capacity (see Shuter 1990 for analytical solution), but for fished populations this is an equilibrium density where the productive capacity of the population is balanced with fishing mortality (Fig. 2; e.g., Paulik 1973). The change in equilibrium density or carrying capacity is a commonly used measure of "success" or "cost" of habitat alterations (e.g., Bovee 1981; Orth and Maughan 1982).

Another feature of the stock–recruitment relationship is the maximum level of recruitment. For fish populations where density-dependent population regulation occurs at the young-of-the-year stage, the maximum recruitment is a useful measure for comparing the productive capacity of different habitats.

The final feature we will discuss is the distance that the recruitment line is above or below the replacement line (Fig. 2). This distance represents surplus production and determines the rate at which the population will grow or decline at a given stock size (Fig. 5; Paulik 1973). To illustrate how surplus production is important for fish population dynamics, consider the population trajectory of a hypothetical population over time (Fig. 5). If the stock–recruitment relationship is altered so that the carrying capacity remains the same, but surplus production is increased, the population will reach the same equilibrium density but will approach this density more quickly (Fig. 5). In nature, carrying capacity would also likely increase, but this hypothetical example demonstrates the effect of surplus production by itself. The amount of surplus production thus determines how quickly a population can grow and how quickly the population responds to a perturbation, habitat enhancement, or alteration. Also, the amount of surplus pro-

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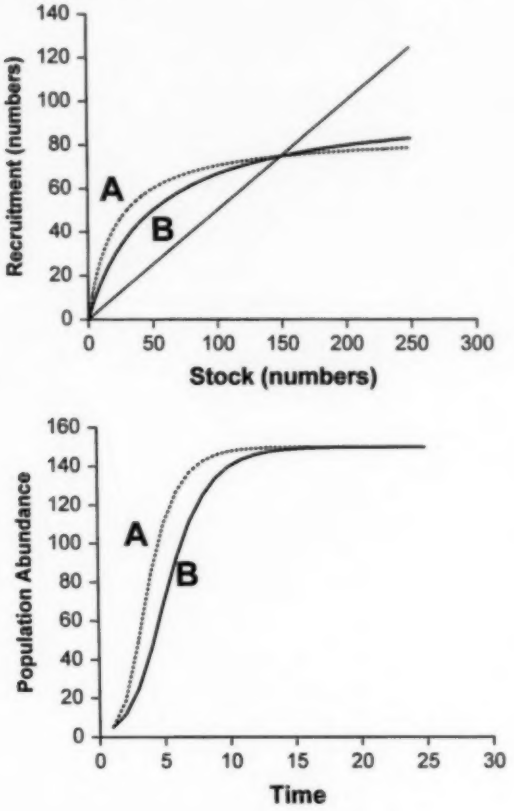
Fig. 5. The effect of varying surplus production on the dynamics of hypothetical fish populations. The upper panel illustrates two fish populations (A and B) with the same carrying capacity, but with population A having a greater surplus production than B. The lower panel shows that population A grows more quickly than population B from the same starting point and with the same equilibrium density.

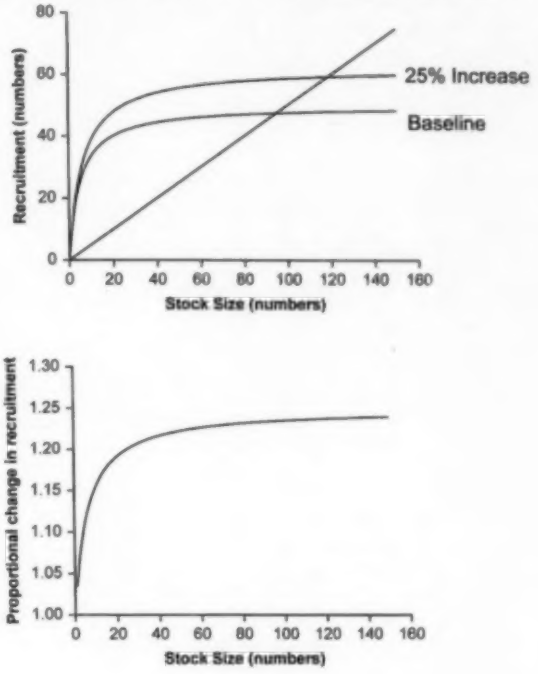


duction is important in determining the potential harvest from an exploited fish population (e.g., Ricker 1975).

A case study of lake whitefish (*Coregonus clupeaformis*)

To illustrate how habitat variables can be linked to population-level processes, we will use an example based on lake whitefish. As shown by Taylor et al. (1987), the recruitment process of lake whitefish is a three-step process: egg deposition (which depends on spawning stock biomass), overwinter egg survival, and early spring larval survival. In this example, we will assume that density-dependent population regulation occurs only at the young-of-the-year stage. For lake whitefish, the survival of eggs depends largely on substrate size and the amount of ice cover during the winter (Taylor et al. 1987; Brown et al. 1993). Freeberg (1985) found that egg survival in an ice-free year in Grand Traverse Bay, Michigan, was highest at a depth of 1.5 m where coarse substrate predominated, and was nearly zero at other depths where the substrate was finer.

Fig. 6. The stock–recruitment relationship for lake whitefish under baseline conditions and under a 25% increase in the amount of suitable spawning substrate. The lower panel shows the percentage increase in recruitment as a function of stock size.



Considering only the egg stage, an idealized stock–recruitment relationship for this stock follows a Beverton–Holt stock–recruitment curve (Fig. 6; Beverton and Holt 1957), with suitable substrate being a limiting factor. The stock–recruitment curve follows the Beverton–Holt form because there is a limited amount of suitable substrate, resulting in an asymptote to the maximum level of recruitment (Beverton and Holt 1957; Ricker 1975). In this case, spawning habitat is a consumable habitat component, but we are assuming that it is not dynamically affected (i.e., that the quality of the habitat is not affected by high levels of spawning). If the amount of suitable spawning area is augmented from this baseline (e.g., increased by 25%), the curve would be shifted upwards to reflect the greater number of recruits that could be produced at a given level of stock size (Fig. 6). Coinciding with the 25% increase in spawning habitat, the maximum recruitment, maximum surplus production, and carrying capacity all increase by 25% (Table 1). In this example, the percentage increase in each of these metrics is similar because the replacement line intersects the recruitment curves after they have flattened out, and are nearly parallel (Fig. 6). In contrast, changes in recruitment are small at low stock sizes but increase to a maximum of 25% at high stock sizes. This pattern occurs because spawning substrate is not the primary limiting factor at low stock sizes, but with increasing stock size it becomes more limiting to recruitment (i.e., egg survival is density dependent).

After the egg stage, survival of young whitefish is highly dependent on their growth rate (Taylor et al. 1987). Taylor and

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Table 1. Response of a fish population to hypothetical habitat changes.

Population response	Percent increase	
	Increase spawning habitat by 25%	Increase zooplankton production
Maximum recruitment	25.0	25.0
Equilibrium density	25.0	57.6
Maximum surplus production	25.0	20.6
Stock size where surplus production is maximized	25.0	35.5

Fig. 7. Survival of larval lake whitefish as a function of number of eggs hatching and spring zooplankton abundance (from Freeberg 1985).

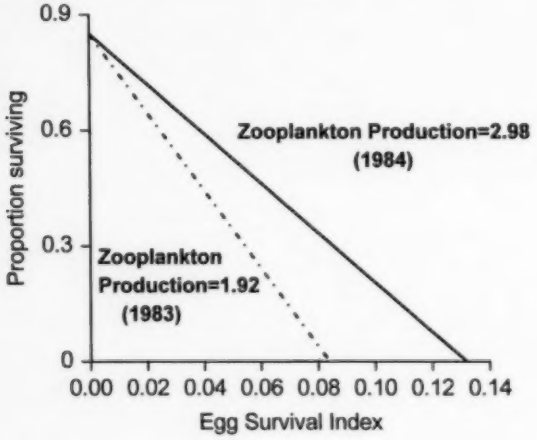
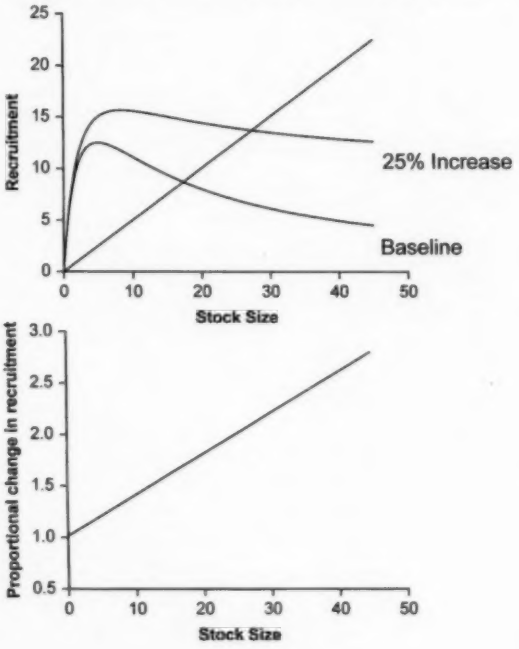


Fig. 8. The stock–recruitment relationship for lake whitefish under baseline conditions and for a scenario where zooplankton productivity is increased to result in a 25% increase in the maximum level of recruitment. The lower panel shows the percentage increase in recruitment as a function of stock size.



Freeberg (1984) found that the zooplankton to fish ratio was a good predictor of growth and survival of larval whitefish and that the survival of larval whitefish varied between years with different levels of zooplankton productivity (Fig. 7; Freeberg 1985). When the survival rate declines linearly with initial cohort size (Fig. 7), the stock–recruitment curve follows the Ricker (1954) rather than the Beverton–Holt form (Fig. 8; Ricker 1954; Shepherd 1982). In this case, an example of a habitat alteration would be to increase the productivity of the system (e.g., by increasing phosphorus concentration, or by higher water temperature), thereby increasing the zooplankton to fish ratio.

The implications of an increase in zooplankton productivity are more complex than the Beverton–Holt case where population response to habitat change were proportional. If maximum recruitment is increased by 25%, the peak level of surplus production increases by only 20.5% (Table 1). This occurs because the peak in surplus production occurs at a stock size 35.5% greater than in the baseline case. Further, the equilibrium density increases substantially more than recruitment, being 57.6% higher than the baseline case (Table 1).

The previous example illustrates the effects of varying single factors on the stock–recruitment relationship. In both these cases, the form of the relationship was maintained (i.e., Ricker vs. Beverton–Holt), but the height of the recruitment line was increased. In natural systems, several factors limiting recruitment often vary simultaneously. In addition to quantity of spawning substrate and zooplankton production, larval whitefish survival also varies with the extent of ice cover during the winter (Taylor et al. 1987; Brown et al. 1993). During winters where ice cover is extensive, the eggs are protected from damaging waves and water currents and their survival is greater for all depths and substrates up to 6 m of water depth (Freeberg 1985). When the effects of annual variation in ice cover are combined with changes in zooplankton production, both the height and shape of the recruitment line varies (Taylor et al. 1987). When the recruitment line changes both height and shape, the population response also varies across the measures (i.e., equilibrium density, surplus production, maximum recruitment) portrayed above. This reinforces the conclusion reached for the Ricker stock–recruitment curve that a population responds to habitat alterations in different ways for the different measures available in the analysis of stock–recruitment relationship.

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Discussion

It has long been known that, to have a good fishery, you must have good habitat. However, it has only been in the last two decades that a concerted effort has been made to define and quantify habitat for fish populations. Our view is that the habitat requirements for a fish population are directly related to the requirements for an individual's growth and survival, i.e., its niche. The intersection of the niche and the environment defines the utility of a habitat for a species. Thus, production by a fish population is a function of how closely the niche of an individual is realized by the environmental conditions in which it resides. It is important to note that an individual organism's niche varies over time and between individuals because of their genotype, phenotype, and acclimation history (Shuter 1990). As such, habitat requirements can vary for an individual over its life and can vary between individuals of the same species. If the biotic and abiotic requirements are at optimal levels, based on the genetic makeup of the population, then growth and survival of fish in the population would be maximized.

When evaluating the habitat requirements of a fish population, it is important to identify whether these are consumable or nonconsumable resources and if they are dynamically affected or not by the population itself. This categorization determines whether the population will respond in a density-dependent or density-independent manner to habitat alterations and the time needed for population responses to occur. In our example, the response of fish growth and survival to habitat alterations will vary between these resource categories. Even within a category, the population response will differ among habitat components, depending upon the degree to which they are a limiting factor. Quantification of the shape of these population dynamic response functions for each of these habitat categories is essential for fisheries professionals to design appropriate habitat management plans. Additionally, such information will allow managers and policy makers to better predict the impact of habitat alterations to the production dynamics of a fish population. This can only be done by approaching habitat analysis from a holistic viewpoint that includes not only the physical and chemical components of habitat but also the biological components. An evaluation of one without the other will prove of little use to fisheries managers as it is the interaction between the two components that creates the production potential for the fish population.

An example of the importance of the synergism between biotic and abiotic habitat components in determining the fish production potential in a specific body of water is the substitutability of food and temperature resources. A major effect of temperature is to alter the growth rate of fishes. Likewise, food abundance affects fish growth rate. As such, changes in thermal habitat can be offset or "substituted for" by changes in food abundance. Thus, if the expected growth response of fish in an altered thermal habitat is not manifested, it may be due to changes in food abundance. Attempts to focus on only the biotic (food resource) or the abiotic (temperature) components of habitat would provide an inadequate and inaccurate view of the relationship of the environment to fish production.

For lake whitefish, it is clear that changes in surplus production did not match the changes in equilibrium density. This result shows that changes in sustainable harvest are not predictable from estimated changes in equilibrium density. As such, the costs or benefits of a habitat alteration in terms of yield to fishermen are not apparent from changes in predicted equilibrium density. Thus, changes in the production dynamics of a population in relation to changes in habitat quality and quantity is an important measure beyond static measures of standing crop (i.e., number per square meter) when evaluating benefits or costs of habitat alterations.

In summary, the population dynamics of a fish population are the ultimate measures of the quality and quantity of its habitat, as growth, survival, and reproduction are directly related to requirements for specific abiotic and biotic resources. We portrayed this relationship using stock–recruitment functions. An important finding is that there is no single "best" measure of the impact of habitat alteration on a fish population. The density-dependent response of a species depends upon its biology and the way that habitat alteration affects its vital rates. Further, habitat alterations do not necessarily alter all population characteristics to the same extent. For example, relatively small changes in recruitment can substantially change carrying capacity, while producing a small change in the surplus production of the population. Pragmatically, this means that the impact of a habitat altering action needs to be evaluated across several population-level descriptors. For exploited populations, surplus production is perhaps most important because it determines the level of harvest that a population can sustain. The equilibrium density is also important for such species, since this will determine the abundance the angler will perceive and determine catch per effort. For unexploited species managed for high levels of abundance, the equilibrium density is probably the most important population characteristic to compare if the goal is to increase abundance. For species at low levels of abundance or threatened and endangered species, the change in recruitment and surplus production at low stock levels would be the most appropriate responses to compare. Thus, the approach we propose is useful in linking the characteristics of the environment to the population dynamics of a species at all levels of abundance.

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Detecting changes in the nearshore fish community

N.P. Lester, W.I. Dunlop, and C.C. Willox

Abstract: The response of a fish community to a change in habitat can be measured only if an assessment of the community is done before and after the change. Decisions must be made about how many years of data will be collected and how many samples per year. We show how these sampling requirements are determined for index fishing surveys that use a spatially random sampling design. The methods are illustrated using trapnetting data of common species (e.g., rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), smallmouth bass (*Micropterus dolomieu*), and white sucker (*Catostomus commersoni*)) on five lakes (208 –72 500 ha). The results indicate that, for a sampling intensity of 45 sets per yr, 7 yr of sampling before and after the change would be needed to detect a twofold change in abundance of any species (one-tailed *t*-test, $\alpha = 0.05$ and $\beta = 0.10$). This sampling requirement cannot be greatly reduced by increasing the number of sets per year because the among-year variance component is large. Evaluating the effects of habitat changes within a shorter period would require improvements in sampling method that reduce the annual variation in catchability. Alternatively, if similar effects occur in several lakes, the required number of years could be reduced by analyzing lakes as a group rather than individually.

Résumé : La réaction d'une communauté de poissons à une modification de l'habitat ne peut être mesurée que si la communauté fait l'objet d'une évaluation avant et après la modification. Cette évaluation nécessite une décision quant au nombre d'années sur lesquelles doit porter la collecte des données et au nombre d'échantillons à prélever chaque année. Nous présentons la manière de fixer ces exigences dans le cas de pêches indicatrices à plan d'échantillonnage spatialement aléatoire. Les méthodes utilisées sont illustrées par des données portant sur la capture au filet-trappe d'espèces communes (crapet de roche, crapet-soleil, achigan à petite bouche, meunier noir, etc.) dans cinq lacs (208 à 72 500 ha). Les résultats obtenus montrent que, pour une intensité d'échantillonnage de 45 ensembles par année, il faut sept années d'échantillonnage avant et après la modification pour pouvoir détecter un changement du simple au double dans l'abondance de toute espèce (test t unilatéral, $\alpha = 0{,}05$ et $\beta = 0{,}10$). On ne peut diminuer sensiblement ce nombre d'années en augmentant l'intensité d'échantillonnage, car la composante inter-années de la variance est importante. Pour pouvoir évaluer les conséquences de la modification en moins d'années, il faudrait améliorer la méthode d'échantillonnage de manière à réduire la variation annuelle de la capturabilité. Si plusieurs lacs manifestent des effets semblables, une autre façon de diminuer le nombre d'années requises consisterait à traiter ces lacs en groupe plutôt qu'individuellement.
[Traduit par la Rédaction]

Introduction

Index fishing programs are used to evaluate the effects of habitat change and other human impacts on the abundance of fish. To test whether the fish community responds to a change in habitat, indexing must be done before and after the change occurs. This approach is based on the premise that the catch (c) of a species is related to fish abundance (N) as $c = qfN$, where f is the amount of effort and q is catchability of the gear for that species. In well-designed surveys, units of effort are standardized so that f refers to the number of sampling occasions and mean catch ($\bar{c} = c/f = qN$) serves as an index of abundance. In planning the study, one must decide what index fishing method will be used, how many years of data will be obtained before and after the perturbation, and how much sampling will be done each year.

The sample size required depends in part upon the anticipated magnitude of change (d), the specified significance level (α), the desired power ($1 - \beta$), (i.e., probability of detecting this difference if it exists), and the index fishing method. Initially, the most important question is what method will be used because any estimation of sample size requires information about the sampling variance of the method. Once variance has been determined from historical data, one can calculate the sample size needed to detect a specified amount of change at specified significance and power levels.

In this paper, we develop a sample size formula for a trapnet survey method that has recently been proposed as a standard technique for assessing the nearshore fish community of Ontario lakes (Willox and Lester 1994). This standard, known as Nearshore Community Index Netting (NSCIN), was defined in 1991 when it was acknowledged that a lack of index fishing standards in Ontario compromised the value of histori-

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Table 1. Standards for nearshore community index netting.

Parameter	Target	Acceptable range
Season	After 1st week in August and before 13°C surface temperature	
Gear	1.8-m trap nets	
Set duration (h)	24	
Net separation (km)	0.5	
Site selection	Random	
Reuse of sites	None	After 2 nights
Depth of water at gap (m)	2.0–2.5	1.7–3.5
Lead length in water (m)	46	30–46
Lead to shore distance (m)	0 (i.e., on shore)	0–20
Water depth at end of lead (m)	0	0–1.0
Lead angle from shore	90°	70–90°

cal data (Lester et al. 1991). The diversity of methods that had been used, often for a common purpose, not only rendered multiple lake comparisons ineffective, but also failed to supply the comparable data needed to design better experiments.

Methods

The NSCIN method, described in detail by Fulford (1993), established standards for gear type, sampling season, selection of sites, and time and duration of sets (Table 1). The 1.8-m trapnets offer a nondestructive method of sampling the adult life stages of the nearshore species. These nets are set overnight at randomly determined sites that meet criteria listed in Table 1. The sampling season (from the second week in August until surface temperature drops to 13°C) typically offers a 6- to 7-wk period within which sampling may be done, at a time when spawning does not affect spatial distribution.

Calculation of the sampling required to detect a change in abundance requires information about among-year and within-year variability. Among-year (i.e., annual) variation in estimates of abundance is expected, partly because abundance fluctuates because of natural variation in recruitment and mortality, but also because catchability may vary depending on factors such as weather conditions during the sampling period. The sample size in years must be large enough to detect change against this backdrop of annual variation. Several years of pretreatment data are needed, therefore, to describe the average abundance and establish a baseline for assessing whether a change in abundance occurs. Although the annual variability in abundance estimates during this phase of the experiment will indicate how many post-treatment years of data are needed (e.g., Vaughan and Van Winkle 1982; Trautman et al. 1985), this variability will depend on the within-year variability of catches and the sample sizes used to obtain abundance estimates. If sampling intensity is low, estimates of abundance will be subject to a large sampling error that will inflate the observed variability among years. Consequently, many years of study might be needed to detect a change in abundance. On the other hand, if sampling intensity is high, more precise annual estimates will be obtained, among-year variance will be lower, and a change in abundance could be detected with fewer years of study.

Assuming that catches, appropriately transformed, meet the assumptions of a *t*-test, we can predict the required combination of sample sizes as follows. For a species, the required number of years in each phase of the experiment (n_1) depends on the expected variance among yearly estimates of abundance (s_1^2) and the desired detectable change in abundance (d), as well as Student t values that vary with the significance level (α) and the power ($1-\beta$) of the test:

$$(1) \qquad n_1 = \frac{2(t_\alpha + t_\beta)^2 s_1^2}{d^2}$$

(Zar 1984). Because mean catch is estimated in two stages, where years are the primary unit and sites are the secondary unit, the expected variance among years (s_1^2) is

$$(2) \qquad s_1^2 = V_1 + \frac{V_2}{n_2}$$

where V_1 is the among-year variance component, V_2 is the within-year variance component (i.e., among sites) and n_2 is the number of sites sampled per year (Cochran 1977). Substituting for (s_1^2) in eq. 1, the sample size formula becomes

$$(3) \qquad n_1 = \frac{2(t_\alpha + t_\beta)^2}{d^2}\left(V_1 + \frac{V_2}{n_2}\right)$$

We use NSCIN data from five lakes to estimate variance components (V_1, V_2) and develop an explicit formulation of eq. 3 to estimate the number of years (n_1) to detect a given change in abundance (d) for a range of sampling intensities (n_2). In doing so, we address the problem of what transformation of the data is needed to meet assumptions implicit in this theory (e.g., normal distributions, homogeneous variance). Normal distributions rarely apply for index catch data, and almost invariably, the variance of the catch increases with the mean (Eberhardt 1978; Elliott 1971; Green 1979). We show that this is also the case for our data and that a logarithmic transformation effectively deals with these problems, at least for frequently captured species.

Sources of data

Multiple years of NSCIN data were available from five lakes (Table 2) to estimate the variance properties of this survey method. Three years of data were available from two lakes (Simcoe and Joseph) and 2 yr from three lakes (Buckhorn, Drag, and Dickey). Survey methods followed the protocol described above (see Table 1). Except for Simcoe, whole lake surveys were conducted with suitable sites selected at random along the shoreline of the lake. On Simcoe, sampling was restricted to a southern portion of the lake that spanned a shoreline length of approximately 100 km, about 40% of the total lake shoreline. Although all surveys were conducted within the sampling season specified in Table 1, the sampled portion of this season varied among lakes (Table 2). For example, surveys on Simcoe were conducted during the last 3 wk of August, but surveys on Drag and Buckhorn spanned the last 2 wk in September. Consequently, the range in surface temperatures at the time of sampling varied among lakes (Table 2). Sampling intensities were similar among lakes, resulting in a mean of 45 sets per year.

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Table 2. Lakes, lake sizes, survey dates, water temperature ranges, and number of sets per survey.

Lake name	Surface area (ha)	Shoreline length (km)	Survey year	Survey dates	Temperature range (°C)	No. of sets
Lake Simcoe	72 500	250	1991	Aug. 8 – Aug. 29	26–20	47
			1992	Aug. 10 –Aug. 28	24–18	48
			1993	Aug. 9 –Aug. 31	27–20	45
Lake Joseph	5375	209	1991	Sept. 11 – Sept. 27	21–14	48
			1992	Sept. 9 –Sept. 25	20–16	48
			1993	Sept. 8 –Sept. 24	20–15	48
Buckhorn Lake	3189	112	1992	Sept. 14 – Oct. 2	21–12	44
			1993	Sept. 7 –Sept. 30	21–11	36
Drag Lake	1003	41	1992	Sept. 14 – Oct. 2	19–13	60
			1993	Sept. 20 –Oct. 1	17–12	39
Dickey Lake	208	18	1992	Aug. 25 – Sept. 11	25–17	39
			1993	Aug. 30 –Sept. 17	24–18	42

Species and sizes of fish captured

Commonly captured species included rock bass (*Ambloplites rupestris*), pumpkinseed (*Lepomis gibbosus*), bluegill (*Lepomis macrochirus*), smallmouth bass (*Micropterus dolomieu*), largemouth bass (*Micropterus salmoides*), white sucker (*Catostomus commersoni*), brown bullhead (*Ameiurus nebulosus*), yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*). These species accounted for greater than 99% of the catch in each lake (Fig. 1). The species composition in Buckhorn differed markedly from the other four lakes. In Simcoe, Joseph, Drag,and Dickey, catches were dominated by rock bass, pumpkinseed, smallmouth bass, and white sucker. In Buckhorn, these species accounted for only 5% of the catch and the dominant species included bluegill, walleye, and largemouth bass. The gear captured a broad spectrum of size- and age-classes. Examples of the size and age composition for the four most dominant species are shown in Fig. 2. Size of fish typically ranged from about 100 mm fork length up to the maximum size expected for each species. Age compositions often included age 1 fish, but the highest catches were observed at intermediate ages.

Transformation of catches

The within-year variance-mean relationship was examined to determine what type of transformation would be needed to apply parametric methods of analysis. For each mean catch shown in Fig. 1*a*, we calculated the variance and plotted these against the mean (Fig. 3*a*). Variance increased markedly with the mean. For small mean catches, variance was approximately equal to the mean, but for larger mean catches (i.e., >1.0) variance increased roughly in proportion to the square of the mean. The latter relationship implies that for larger means a logarithmic transformation is needed to stabilize variance (Taylor 1961). Because some catches were zero (even for the most frequently captured species), we added a constant to the raw catches. We used $y = \log_{10}(x + 1)$, where x refers to the raw catch.

Variances and means of the log-transformed data (Fig. 3*b*) indicated that this transformation was effective in stabilizing variance, at least for larger means. For means >0.2 on the log scale, the average variance was 0.2, and there was no marked tendency for variance to increase with the mean. For means <0.2, variance decreased rapidly, approaching zero as the mean catch approached zero.

A more instructive way of demonstrating the effect of this transformation is comparing arithmetic means (*AM*) and geometric means (*GM*) after adding a value of 1 to the catch (Fig. 4). Geometric means are the back-transformed values of means calculated on a logarithmic scale. When a logarithmic transformation is effective in stabilizing variance, the expected relationship between these means is

$$(4) \quad \log_{10} AM = \log_{10} GM + 1.15\, s^2$$

where s^2 is the variance of the log-transformed data (Elliott 1971). Substituting for $s^2 = 0.2$ and taking antilogarithms yields:

$$(5) \quad AM = 1.70\, GM$$

Individual estimates of the arithmetic and geometric means follow the predicted relationship once the arithmetic mean exceeds a value of about 2 (Fig. 4). Because this arithmetic mean resulted from adding 1 to each catch observation, it corresponds to an arithmetic mean of 1 (i.e., 2 – 1) for the raw data. In other words, the logarithmic transformation, $y = \log_{10}(x + 1)$, is effective in stabilizing variance for cases where mean raw catch exceeds a value of 1. For this reason, analyses which are based on log-transformed data ignored species for which mean raw catch in any year within a lake was less than 1.0.

Estimation of variance components

Estimates of the within-year and among-year variance components of frequently captured species were calculated as follows. For a species in a lake, means and variances for the log-transformed catch data were calculated for each year. The average variance supplied an estimate of the within-year variance component (V_2). The variance among years (s_1^2) was then calculated from the yearly mean log-catch values and this was used to estimate the among-year variance component (V_1) by rearranging eq. 2:

$$(6) \quad V_1 = s_1^2 - \frac{V_2}{n_2}$$

where n_2 is the number of sets per year. The significance of this variance component was tested using an *F*-ratio of

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Fig. 1. Catch results by lake, species, and year: (a) the arithmetic mean number of fish caught per set (mean catch); (b) the proportion of sets that caught at least one fish. Bar shading indicates year: 1991 (solid); 1992 (hatched); 1993 (open). Labels on the *x*-axis indicate species: RB, rock bass; Pu, pumpkinseed; SB, smallmouth bass; WS, white sucker; BB, brown bullhead; LB, largemouth bass; YP, yellow perch; Bl, bluegill; Wa, walleye.

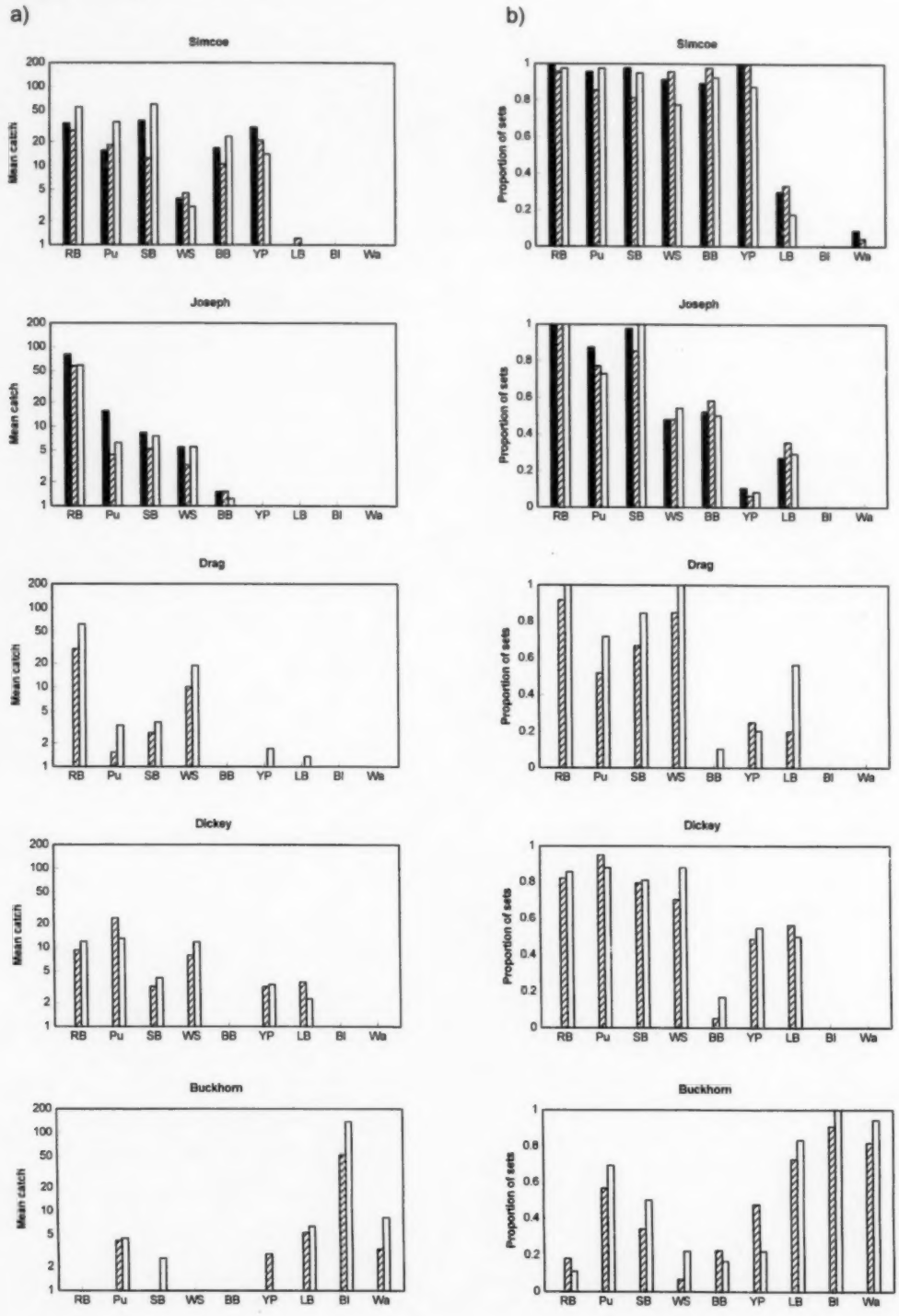

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Fig. 2. Size and age compositions of the catch of rock bass, pumpkinseed, smallmouth bass, and white sucker from Lake Simcoe and Lake Joseph in 1992.

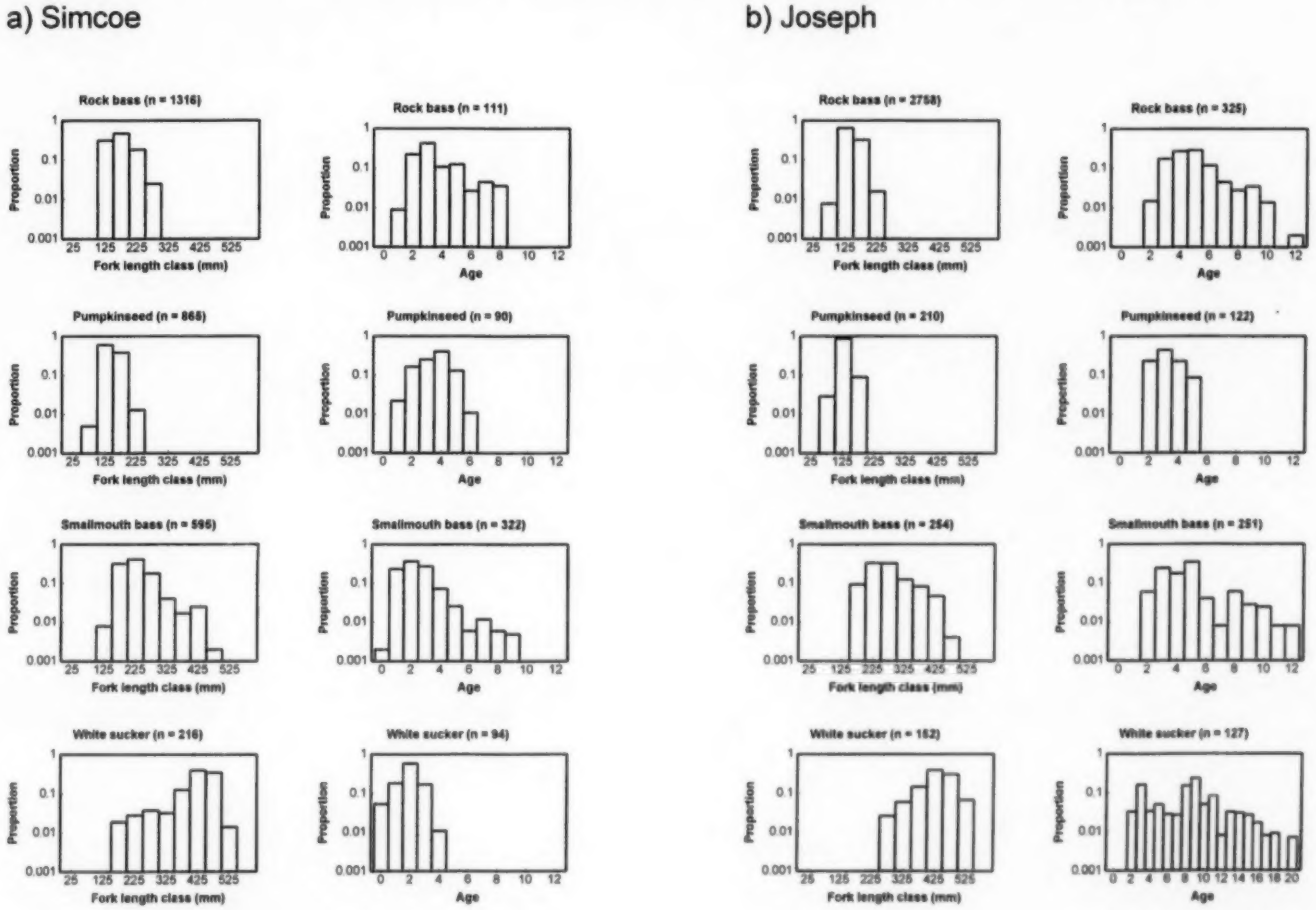
a) Simcoe
b) Joseph
Rock bass (n = 1316)
Rock bass (n = 111)
Rock bass (n = 2758)
Rock bass (n = 325)
Pumpkinseed (n = 868)
Pumpkinseed (n = 90)
Pumpkinseed (n = 210)
Pumpkinseed (n = 122)
Smallmouth bass (n = 596)
Smallmouth bass (n = 322)
Smallmouth bass (n = 254)
Smallmouth bass (n = 251)
White sucker (n = 216)
White sucker (n = 94)
White sucker (n = 152)
White sucker (n = 127)
Proportion
Fork length class (mm)
Age

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Fig. 3. The relationship between within-year means and variances of catches for the raw data (a) and log-transformed data (*b*). In (*a*), data are on a logarithmic scale and the relationship (for means >1) is described by a power function (dotted line): variance = $2.87(\text{mean})^{1.82}$, r^2 = 0.92, n = 66. In (*b*), means and variances were calculated after a $\log_{10}(x + 1)$ transformation (where x refers to the raw catch). The solid line (variance = mean) supplies a reference for the effect of this transformation. Species are as in Fig. 1.

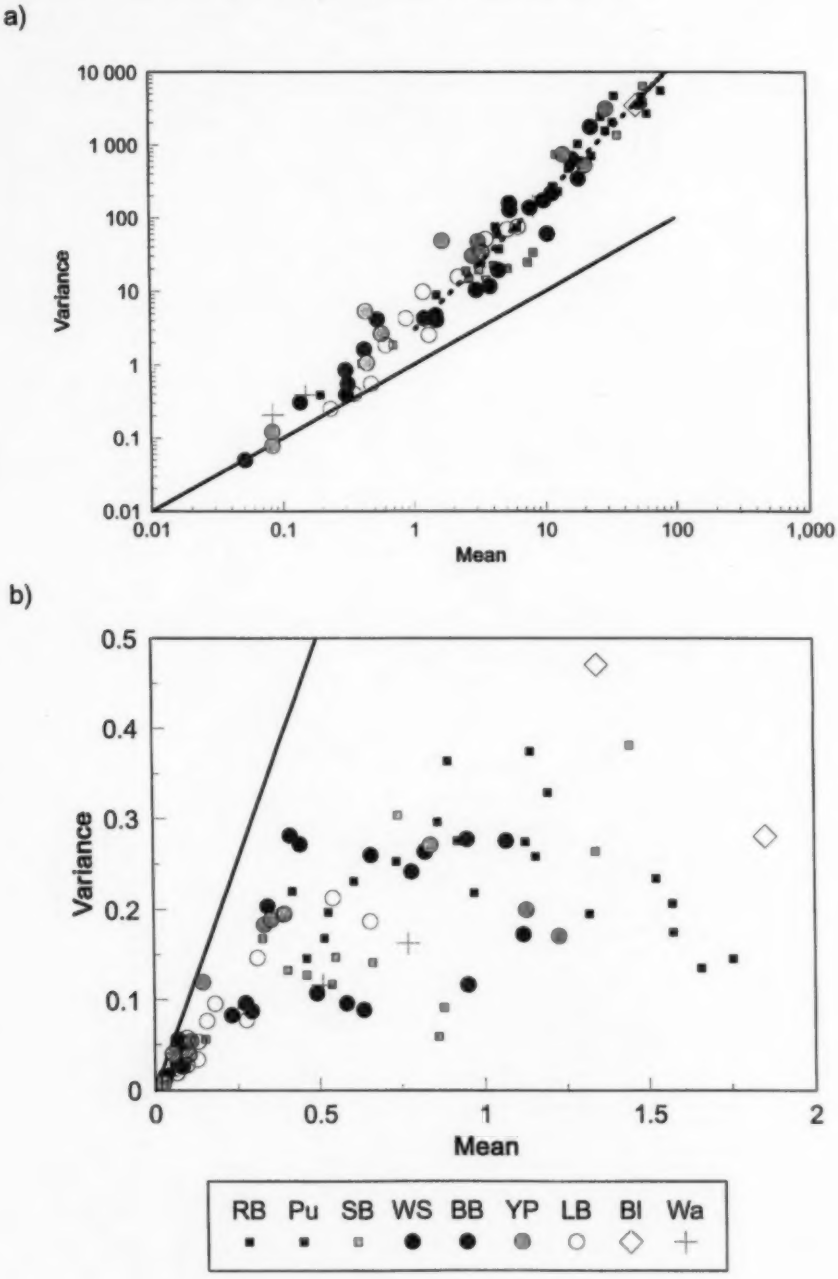

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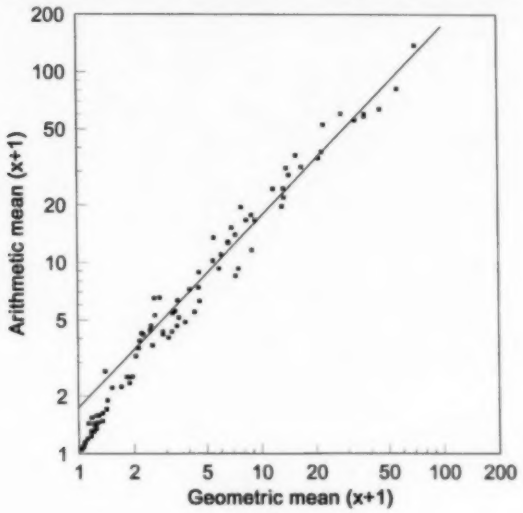
Fig. 4. The relationship between arithmetic means and geometric means of yearly catches after adding a value of 1 to the raw data.



$n_2 s_1^2/V_2$. For cases where n_2 varied among years, the harmonic mean was used.

Table 3 shows, for each species in each lake, the mean of yearly log-catch means, the observed among-year variance (s_1^2), estimates of variance components (V_1, V_2), and the significance of the among-year component (p). Average estimates for each species were calculated by averaging across lakes (columns). These are shown in the last column of Table 3. Similarly, average estimates for each lake were calculated by averaging across species (rows) and these are shown in the last row. An overall average estimate of each component (i.e., average of all species and lakes) is shown in the bottom right cell.

The overall average estimates indicated a within-year variance of 0.2065 and an among-year variance of 0.0264. These estimates assume differences among lakes and species did not exist, but these hypotheses are difficult to test because data are not available for all combinations of lakes and species. Furthermore, because estimates are based on only 2 or 3 yr of observation, only large differences could be detected. Pooled estimates of the within-year component (V_2) are typically around 0.2 for each species and no obvious relation with lake size exists.

Estimates of the among-year component (V_1) were highly variable, ranging from –0.0041 to 0.1369, but this is not surprising given that individual estimates were based on only 2 or 3 yr of data and are, therefore, subject to a large sampling error. The F-ratio tests indicated this component was significant in 15 of 25 cases and that a significant value was more frequently obtained for lakes that were sampled for more than 2 yr. This difference is expected, partly because statistical power increases with sample size, but also because sequential estimates of abundance are not independent and the among-year variance component is expected to increase with the length of the time series and then reach an asymptote. Considerably longer time series would be needed to obtain accurate and precise estimates of the among-year component so that species and lake differences could be compared. With our data, such comparisons are not warranted.

Sample size requirements

We used the average estimates of variance components to calculate how much sampling would be needed to detect a change in the abundance of a species following a change in habitat. Given the general sample size formula for a t-test (eq. 3) and substitutions for the variance components (V_1 = 0.0264; V_2 = 0.2065) from Table 3, we obtained the formula:

$$(7) \quad n_1 = \frac{2(t_\alpha + t_\beta)^2}{d^2}\left(0.0264 + \frac{0.2065}{n_2}\right)$$

where n_1 refers to the number of years before and after the management action and n_2 refers to the number of trapnet sets per year. Because variances were determined for log-transformed data, the detectable change is also measured on this scale. Its value is the difference between the mean annual log catch before and after the management action. The implication in terms of a change in abundance is revealed by noting that d is simply the logarithm of the ratio of geometric means. That is, since geometric means in each phase (GM_1, GM_2) are the back-transformed mean log catches:

$$(8) \quad d = \log_{10} GM_2 - \log_{10} GM_1$$

and thus:

$$(9) \quad d = \log_{10} \frac{GM_2}{GM_1}$$

or simply;

$$(10) \quad d = \log_{10} R$$

where R is the ratio of geometric means. Since arithmetic means are proportional to geometric means (see Fig. 4), this ratio can also be interpreted as the ratio of arithmetic means, or simply the ratio of abundances. Substituting for d in eq. 8 yields

$$(11) \quad n_1 = \frac{2(t_\alpha + t_\beta)^2}{(\log_{10} R)^2}\left(0.0264 + \frac{0.2065}{n_2}\right)$$

In this format, the sample size equation indicates the amount of sampling needed to detect an R-fold change in abundance.

To demonstrate the implications of this formula we calculated the detectable change in abundance (R) for a variable number of years (n_1 = 3–10) and a variable number of sets per year (n_2 = ∞, 45, 20, 10), given a one-tailed test at one significance level (α = 0.05) and three power levels (1 - β): 0.90, 0.80, 0.50. Results for each sampling intensity (n_2) are shown in separate graphs (Fig. 5) that plot the minimum detectable change in abundance (R) as a function of the number of years (n_1).

Figure 5*a* indicates that with 45 sets per year at least 6 yr of data (3 before and 3 after) would be needed to have a 50% chance (i.e. power = 0.50) of detecting a twofold change in abundance at a significance level of 0.05. Substantially more years would be required to test for this effect at more reasonable power levels: 10 yr (i.e., 5 + 5) at power = 0.80 and 14 yr (i.e., 7 + 7) at power = 0.90. Figure 5*b*, which assumes an

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Table 3. Estimates of variance components for log-transformed catch data, $y = \log_{10}(x + 1)$.

Species	Parameter	Simcoe ($n_1 = 3$, $n_2 = 44.8$)	Joseph ($n_1 = 3$, $n_2 = 48$)	Drag ($n_1 = 2$, $n_2 = 47.3$)	Dickey ($n_1 = 2$, $n_2 = 40.4$)	Buckhorn ($n_1 = 2$, $n_2 = 39.6$)	Average
Rock bass	Mean	1.3344	1.6348	1.4020	0.7795		1.2877
	s_1^2	0.0335	0.0109	0.1331	0.0034		0.0452
	V_2	0.2294	0.1757	0.2548	0.2603		0.2301
	V_1	0.0285	0.0072	0.1277	−0.0030		0.0401
	p	<0.01	<0.10	<0.01	NS		
Pumpkinseed	Mean	1.0214	0.6824	0.3625	0.9950	0.4745	0.7072
	s_1^2	0.0247	0.0454	0.0198	0.0349	0.0059	0.0261
	V_2	0.3039	0.2250	0.1203	0.2856	0.2084	0.2286
	V_1	0.0178	0.0407	0.0173	0.0278	0.0007	0.0209
	p	<0.05	<0.01	<0.01	<0.05	NS	
Smallmouth bass	Mean	1.1767	0.8013	0.4715	0.5060		0.7389
	s_1^2	0.1440	0.0143	0.0091	0.0039		0.0428
	V_2	0.3162	0.0973	0.1247	0.1373		0.1689
	V_1	0.1369	0.0122	0.0065	0.0005		0.0390
	p	<0.01	<0.01	<0.10	NS		
White sucker	Mean	0.5709	0.4015	0.9520	0.7430		0.6669
	s_1^2	0.0052	0.0027	0.0564	0.0135		0.0195
	V_2	0.0976	0.2523	0.2073	0.2619		0.2048
	V_1	0.0031	−0.0026	0.0521	0.0070		0.0149
	p	<0.10	NS	<0.01	NS		
Brown bullhead	Mean	0.9916	0.2679				
	s_1^2	0.0046	0.0010				0.6298
	V_2	0.2236	0.0890				0.0028
	V_1	−0.0004	−0.0009				0.1563
	p	NS	NS				−0.0007
Yellow perch	Mean	1.0670			0.3735		0.7203
	s_1^2	0.0402			0.0007		0.0205
	V_2	0.2140			0.1914		0.2027
	V_1	0.0355			−0.0041		0.0157
	p	<0.01			NS		
Largemouth bass	Mean				0.3550	0.6100	0.4825
	s_1^2				0.0035	0.0065	0.0050
	V_2				0.1709	0.1996	0.1853
	V_1				−0.0007	0.0015	0.0004
	p				NS	NS	
Bluegill	Mean					1.6015	1.6015
	s_1^2				0.1275		0.1275
	V_2					0.3757	0.3757
	V_1					0.1180	0.1180
	p					<0.01	
Walleye	Mean					0.6410	0.6410
	s_1^2					0.0338	0.0338
	V_2					0.1395	0.1395
	V_1					0.0303	0.0303
	p					<0.01	
Average	Mean	1.0270	0.7576	0.7970	0.6253	0.8318	0.8087
	s_1^2	0.0420	0.0149	0.0546	0.0100	0.0434	0.0311
	V_2	0.2308	0.1679	0.1768	0.2179	0.2308	0.2065
	V_1	0.0369	0.0113	0.0509	0.0046	0.0376	0.0264

Note: Variance components were estimated only for cases where arithmetic mean catch was above 1.0 in all years. n_1, number of years; n_2, harmonic mean of the number of sets per year; Mean, average of yearly means; s_1^2, variance among yearly means; V_2, average within-year variance; V_1, among-year variance component (calculated as $V_1 = s_1^2 - V_2/n_2$); p, significance of the among-year variance component as tested by the F-ratio ($n_2 s_1^2/V_2$).

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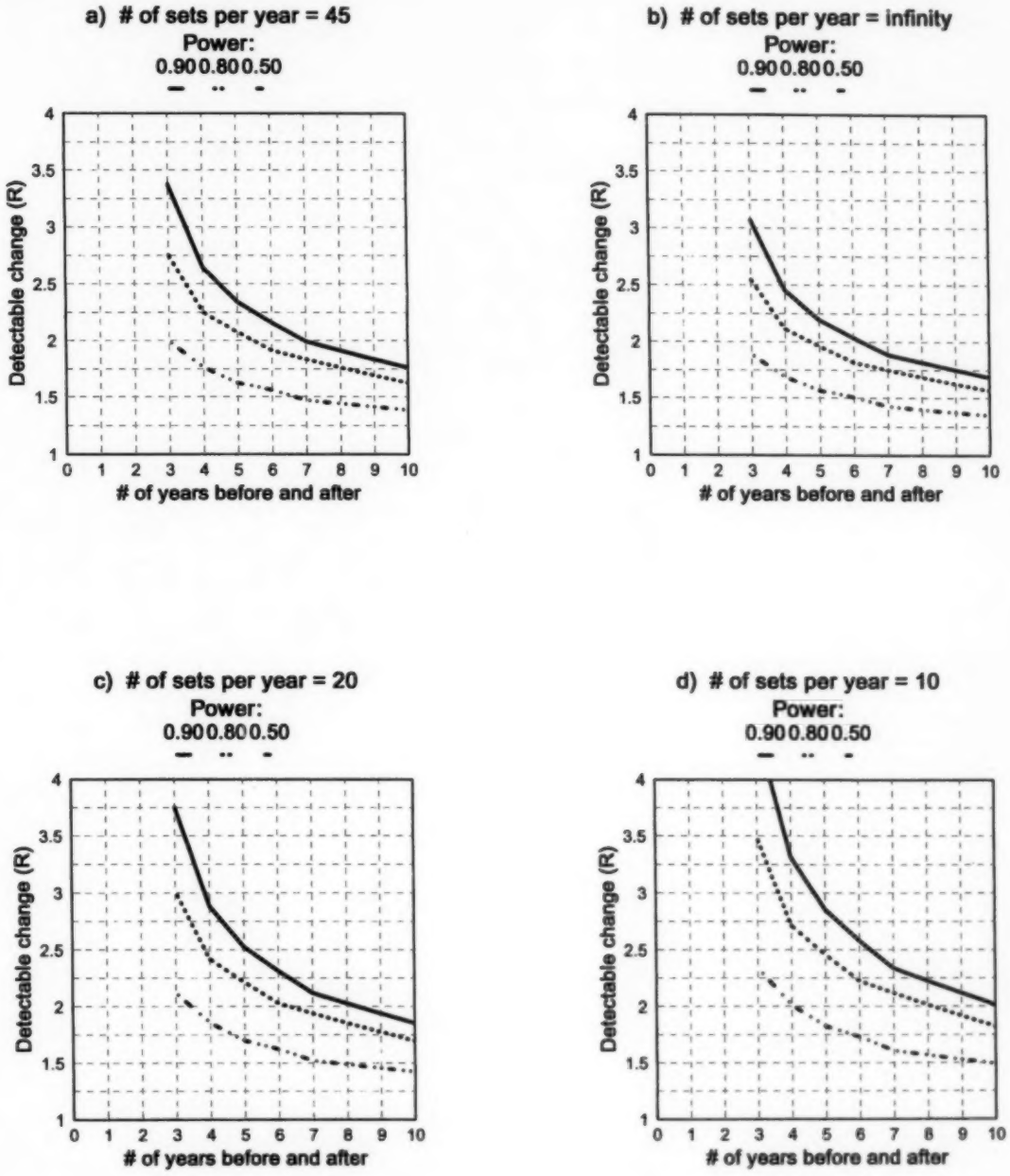
Fig. 5. Estimates of the detectable change in abundance (R) at three power levels (0.50, 0.80, 0.90) as function of the number of years of sampling before and after. Results for different sampling intensities (i.e., number of sets per year) are shown separately: 45 (*a*), infinity (*b*), 20 (*c*), and 10 (*d*).


a) # of sets per year = 45
Power:
0.90 0.80 0.50
Detectable change (R)
# of years before and after
b) # of sets per year = infinity
Power:
0.90 0.80 0.50
Detectable change (R)
# of years before and after
c) # of sets per year = 20
Power:
0.90 0.80 0.50
Detectable change (R)
# of years before and after
d) # of sets per year = 10
Power:
0.90 0.80 0.50
Detectable change (R)
# of years before and after

infinite number of sets per year, indicates that these sampling requirements cannot be greatly reduced by increasing sampling intensity. For example, the total number of years required to test for a twofold change at power = 0.90 is 12 (i.e., 6 + 6). This result implies a reduction of only 2 yr and indicates that the current sampling intensity ($n_2 = 45$) is more than adequate. A more efficient allocation of resources would result from a reduction in sampling intensity. This conclusion is supported by the sample size graphs for $n_2 = 20$ (Fig. 5*c*) and $n_2 = 10$ (Fig. 5*d*). The same test (i.e., twofold change at 0.90

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power) would require a total of 16 yr at a sampling intensity of 20 sets per year and 20 yr at a sampling intensity of 10 sets per year.

Discussion

Peterman (1990) reported that current methods of assessing fish populations have a low probability of detecting a significant change in abundance, should one occur. He used examples drawn from the impact assessment and resource management literature to demonstrate that, because annual variability is typically large, lengthy studies are needed to detect change. Our results agree with this conclusion. The annual variability of abundance estimates (s_1^2) for nearshore species was high and could not be greatly reduced by increasing the within-year sample size. Consequently, study lengths in the order of 10–15 yr would be needed to detect even large changes in abundance (e.g., twofold) by our survey methods.

We expect that sampling requirements will vary depending on the size of lake and species of interest. The life-history characteristics of a species combined with the spatiotemporal heterogeneity of its environment will affect the within-year and among-year variance components that dictate sampling requirements. Such differences could not be detected from our data. Although our analyses were based on a total of 12 lake-years of data, substantially more data are needed to determine whether these components vary among lakes and species. This speaks for the value of standardized index fishing methods. Widespread use of a standard method will result in the accumulation of data needed to better describe its sampling characteristics and better predict the amount of sampling needed to detect changes in abundance. Since the NSCIN method described here has recently been adopted as a standard for assessment of Ontario lakes more precise statements about sampling requirements are expected as its use becomes more widespread. The results to date, however, are in general agreement with other studies.

For trapnet surveys on Lake Erie, Hamley and Howley (1985) reported that detection of a twofold change in abundance following a 7 yr baseline study would take about 3 yr (i.e., total yr = 10). This estimate was based on a sampling intensity of 200 sets per year, a significance level of 0.10 and (since they did not consider power) an implied power of 0.50. Casselman et al. (1986) estimated variance properties for a mixture of index fishing methods and used a simulation model to assess their ability to detect changes in abundance. They concluded that given only 6 yr of baseline data, the chances of detecting even very large changes are small.

The need for long-term studies to test the effects of habitat changes and other human impacts poses two major problems. First, long-term studies require long-term funding, which is difficult to obtain. Second, long-term studies delay the acquisition of knowledge, postponing answers to questions that managers face today. Clearly, any improvement in study design or survey method that could reduce the required length of a study would be welcomed. Here we consider two options: (*i*) modification of sampling methods that might reduce among-year variance and (*ii*) sampling a group of lakes.

The limiting factor dictating the time needed to detect changes in abundance is the magnitude of the among-year variance component (V_1). This component depends on annual fluctuation in abundance caused by recruitment and mortality processes as well as annual variation in catchability. The latter is reduced by standardization of sampling methods (e.g., gear, sampling season, selection of sites, etc.), but wind, water temperature, and light levels are random factors that could affect catches. To judge the extent to which variation in these and other environmental factors affected among-year variance, we need an estimate of the annual variation in abundance of nearshore species. Annual variation in catchability can then be estimated by subtracting the abundance variability from our estimate of the among-year variance component.

We used virtual population estimates of smallmouth bass abundance in Lake Opeongo from 1937 to 1982 (Shuter et al. 1987) to obtain an independent estimate of the natural variation in abundance of a nearshore species (Fig. 6). We calculated variance of the $\log_{10}$ transformed estimates using a 3-yr moving window (i.e., years 1–3, 2–4, 3–5, etc.) and then computed the average variance. This value (0.016) was substantially less than estimates of the among-year variance component (V_1) supplied by our trapnet data (Table 5). For the pooled species estimate ($V_1 = 0.0264$), the difference indicates that 40% of the among-year component may have been caused by annual variation in catchability. For smallmouth bass alone ($V_1 = 0.0390$), our data indicate this contribution may be as high as 60%.

These calculations indicate there is room for improvement in the sampling method. In speculating about changes in method that might reduce annual variation in catchability, we noted that surveys began on approximately the same calendar date each year (within lakes) and were completed within a fairly short period of time (i.e., 2–3 wk; Table 2). Given this short survey period, environmental factors (e.g., weather) that affect catches could be very different in each year. More dispersed sampling over a longer period might result in "average" environmental conditions that are more similar among years and this would be reflected by a smaller among-year variance component (V_1).

Sampling efficiency might be improved by a change in sampling method that reduces annual variation in catchability. If catchability variation could be eliminated, the among-year variance component might be reduced by 40–60%, implying a similar reduction in the required study length. More realistically, however, a change in method might only achieve a fraction of this potential reduction. More may be gained by searching for other means of reducing study length.

If the same habitat alteration occurs in a number of lakes, the number of years needed to detect an effect can be reduced by analyzing lakes as a group rather than individually (e.g., Trautman et al. 1985). The probability of detecting an amount of change then depends on the number of lakes and the number of years sampling each lake. The appropriate statistical procedure is a two-way analysis of variance with lake and time as factors. The amount of data (number of lakes × number of years) needed could be calculated using power tables for analysis of variance (Cohen 1977; Zar 1984), but since we already know the number of years required for a single lake (Fig. 5), it is simpler to use this number to estimate requirements for a group of lakes. The number of years per lake (n_1') needed to achieve the same power as sampling a single lake for n_1 years is given by a formula we derived:

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Fig. 6. Virtual population analysis estimates of population size for age 3 and older smallmouth bass in Lake Opeongo from 1937 to 1982. Data supplied by B.J. Shuter (personal communication).

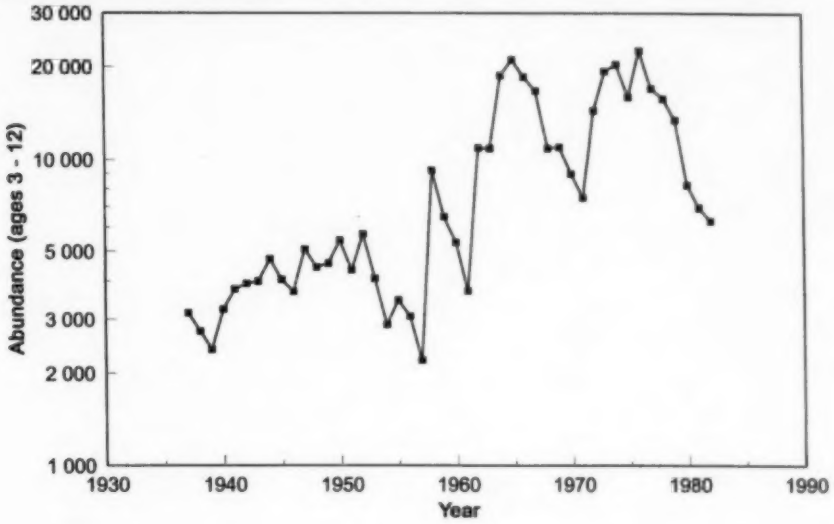

Table 4. Estimated costs of detecting a twofold change in abundance (1 - β = 0.90, α = 0.05) in a single lake and in a group of four lakes.

No. of lakes (n_L)	No. of sets/yr (n_2)	No. of yr (n_1')	Study length ($2n_1'$)	Study cost ($)
1	45	7	14	80 200
1	20	8	16	52 800
1	10	10	20	42 000
4	45	2	4	100 800
4	20	3	6	79 200
4	10	3	6	50 400

Note: Cost estimates are based on eq. 11 where c_1 = $900 and c_2 = $120.

$$(12)\quad n_1' = \frac{n_1}{n_L} + 1 - \frac{1}{n_L}$$

where n_L is the number of lakes. Since the expression on the far right (1 - $1/n_L$) is never greater than 1, the approximate number of years per lake is simply the single lake requirement divided by the number of lakes and then rounded up to the next integer.

Equation 12 assumes that the lakes are good replicates and, therefore, respond in an identical manner to the change that has occurred. For example, this would be the case if abundance of a species decreased twofold in every lake. In practice, this is rare and variation in the size of effect in each lake will reduce power. The calculations presented here are, therefore, minimum estimates of multiple lake sampling requirements.

Increasing the number of lakes not only reduces study length, but may do so without greatly increasing study costs. To demonstrate this, we calculated study costs for a single lake and for a group of four lakes using the following formula:

$$(13)\quad \text{Cost} = 2\, n_L\, n_1\, (c_1 + c_2\, n_2)$$

where c_1 is the fixed cost of implementing a survey (each year on each lake) and c_2 is the cost of one trapnet set. For our sampling method, we estimated c_1 = $900 (staff time for selection of sites, scheduling, and preparation of gear) and c_2 = $120/set (i.e., travel costs plus staff time for sampling and data management). For a single lake (n_L = 1) and a group of four lakes (n_L = 4), we estimated the number of years needed to detect a twofold change in abundance at three levels of sampling intensity (n_2 = 45, 20, 10), power = 0.90, and a significance level of 0.05. For a single lake, these requirements were read from Fig. 5. For a group of four lakes, we used the single lake values and eq. 10 to estimate the required number of years per lake. The costs associated with each scenario are listed in Table 4.

The table shows that sampling at a lower intensity (e.g., 10 sets per year) for a longer period of time is more efficient. The sampling intensity that would minimize costs (n_2^*) can be calculated using the formulae derived for two-stage sampling (Cochran 1977):

$$(14)\quad n_2^* = \left(\frac{c_1 V_2}{c_2 V_1}\right)^{1/2}$$

For our estimates of cost factors and variance components:

$$(15)\quad n_2^* = \left(\frac{900 \times 0.2065}{120 \times 0.0264}\right)^{1/2}$$

giving n_2^* = 7.7, a value close to 10. On a single lake, however, it is unlikely that this optimum sampling intensity would be used because it would require a study length of at least 20 yr. The study length could be reduced to 14 yr if sampling intensity was increased to 45 sets per year, but this would increase assessment costs more than 100% (from $42 000 to $88 200). On the other hand, if 4 lakes were studied using 10 sets per year, the required study length would be reduced approxi-

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mately threefold (from 20 to 6 yr) at a cost increase of only 20% (from $42 000 to $50 400).

We conclude that the most effective way to evaluate the effect of a habitat alteration (or other factor) is to study several lakes at a relatively low sampling intensity. Because the number of years of data required to detect a specified change in abundance decreases as the number of lakes increases, this strategy maintains control over the study length. Given estimates of the within-year and among-year variance components associated with the sampling method, effects could be evaluated on a desired time frame by choosing the appropriate number of lakes. More complex designs, involving control lakes, as well as different treatment times would be needed to attribute a change in abundance to the factor of interest (Green 1979; Walters et al. 1989; Underwood 1994).

A multiple lake design is appropriate for experimental management studies, where actions can be timed to obtain sufficient before and after data. For example, the effects of habitat restoration, stocking and changes in fishing regulations could be studied in this way. Such opportunities do not exist when the goal is to detect the effects of environmental disturbances due to human activities. Pollution, shoreline development, and other forms of habitat degradation are not single events whose timing and magnitude is controllable in most instances. These processes and their effects on populations tend to be gradual and incremental, and the rates of change in fish populations may be so small that statistically significant effects would be detectable only after many years of study. In this case, long-term monitoring of individual lakes is needed. It is important that this monitoring be done in relatively unperturbed areas as well as in perturbed ones. This would obviate the need for specifically acquired before data since it would supply the reference needed to detect when the abundance of fish in perturbed lakes begins to deviate from the range expected in unperturbed systems (Schindler 1987; Underwood 1994).

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Detecting the response of fish to habitat alterations in freshwater ecosystems

Charles K. Minns, John R.M. Kelso, and Robert G. Randall

Abstract: Rushed efforts to repair freshwater ecosystems are obstructing the scientific assessment of successes and failures. Existing ecosystem science is ignored as ecologists plan restoration projects. The problem of detecting fish responses to habitat alterations is reviewed via linked issues: expectations, measures, variability, and scale. Habitat alterations directed at single species populations usually affect other ecosystem components. In the fish community, no single population is the reference point for detecting responses. A set of 15 alternate responses highlights the need for an array of ecological indicators if alternatives are to be distinguished. Potential measures are surveyed. Patterns and sources of spatial and temporal variability are identified. Integrative indicators such as production and community indices may be more suitable for detecting changes as they exhibit less variability. The spatial and temporal scales of ecosystem responses are usually greater than the scales of human interventions and assessment. Guidelines for designing assessments are recommended. Management actions are experiments and must be assessed as such. Learning requires systematic observation with replicates and controls. Restoration plans must focus more on ecosystems and less on preferred species. Given the scales of experimentation required, larger opportunities for useful science must be created by wider coordination, consultation, and cooperation.

Résumé : Les mesures précipitées de restauration des écosystèmes d'eau douce nuisent àl'évaluation scientifique des succès et des échecs. Les écologistes qui planifient ces projets ne tiennent pas compte des connaissances actuelles sur les écosystèmes. Dans le présent article, nous examinons le problème que pose la détection des réactions des poissons aux modifications apportées à leur habitat, selon quatre points de vue interreliés: les attentes, les mesures, la variabilité et l'échelle. Les modifications d'habitat ayant pour cible les populations d'une seule espèce ont généralement un effet sur les autres composantes de l'écosystème. La communauté ichtyenne, qui comprend plus d'une espèce, sert de point de comparaison pour la détection des réactions. Un ensemble de 15 réactions possibles met en relief la nécessité d'utiliser toute une gamme d'indicateurs écologiques si on veut envisager plusieurs solutions distinctes. Nous passons en revue les mesures qui peuvent être utilisées, puis nous relevons les types et les sources de variabilité spatiale et temporelle. Les indicateurs intégrant plusieurs facteurs, comme les indices de production et de communauté, conviennent sans doute le mieux à la détection des changements, car ils sont moins sujets à varier. Par ailleurs, les échelles spatiale et temporelle qui caractérisent la réaction des écosystèmes sont généralement plus grandes que celles où se font les interventions humaines et les évaluations. Nous proposons enfin des lignes directrices pour la conception des évaluations. Toute mesure d'aménagement constitue une expérience et doit à ce titre faire l'objet d'une évaluation. Le progrès des connaissances exige une observation systématique, avec répétitions et témoins. Les plans de restauration doivent porter davantage sur les écosystèmes et moins sur des espèces qu'on entend privilégier. Étant donné les échelles auxquelles les expériences doivent être menées, il faut multiplier les occasions de recherche utile en élargissant la coordination, la consultation et la coopération.
[Traduit par la Rédaction]

Introduction

The scientific dilemma

Whenever society alters habitat within ecosystems to deliberately affect biotic composition and abundance, resource managers and ecologists have, at least, mental models that predict preferred outcomes. Today, in the developed world, there are needs and efforts to restore, remediate, repair, rehabilitate, and rejuvenate freshwater ecosystems damaged as the result of human indifference, ignorance, or choice. Ecologists are being asked to recommend, design, and implement habitat alterations and often must act without the scientific certainty they would prefer.

In the broadest context, ecologists mix politics and science, mix a way of doing with a way of knowing. Politics and science do not mix well. Once the political will to act has been mobilized (possibly by ecologists), society expects actions that produce promised outcomes. Whether or not the scientific knowledge to identify and justify appropriate actions exists becomes a secondary consideration. To be seen to be doing something may be more important than knowing why, or if, it is the right thing to do. Consequently, most of the resources made available for ecosystem restoration have been provided for action. Studying the appropriateness and effectiveness of such actions has a lower priority. Having made a commitment

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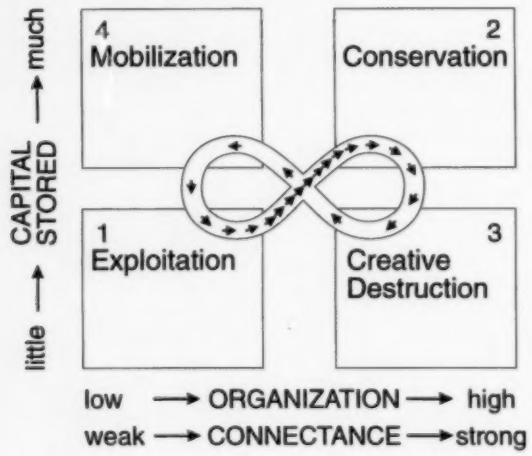
Table 1. Ecological structure, function, and example attributes in hierarchical levels of organization (after Picket et al. 1989).

Level	Structure	Function	Attributes
Individual	Biomass	Physiology, behaviour	Growth, mortality
Population	Density, size structure	Breeding biology, social behaviour	Age structure, genetic structure
Assemblage	Spatial pattern, species composition	Resource levels, competition	Evenness, dominance
Ecosystem	Trophic groups	Energy flow, nutrient flux	Resistance, resilience
Waterscape	Ecosystem types, configuration	Disturbance regime, biotic fluxes	Stability, connectedness

Fig. 1. Holling's (1987) representation of the cyclical connection among four ecosystem functions in relation to the level of stored capital and the degree of connectance/organization. The spacing of the arrows indicates the rapidity of change.



to ecosystems restoration, society expects environmental scientists and managers to produce the expected results quickly without further study. If studies of attempts at ecosystem restoration are inadequate or absent, awkward questions about success or failure can be avoided or ignored. Part of the problem may arise from a failure to recognize two forms of scientific assessment methodology, one designed to enable decision-making now and another designed to provide peer-acceptable conclusive evidence of cause and effect.

Unfortunately, nature can be unforgiving. If actions instituted now turn out to be ineffective or inappropriate, ecosystem restoration will be delayed or fail to match expectations. Awkward questions will resurface. Those questions include the following: (1) How do we know what to fix? (2) How do we know that selected actions are effective or appropriate? (3) Will these actions repair the ecosystem? (4) If actions are applied in new contexts, are they being assessed?

These sorts of questions are not being adequately addressed in the rush to restore ecosystems. Actions often seem to be planned and applied without reference to the existing body of explanatory science. If ecologists and others are to participate in ecosystem restoration efforts, it must be on the basis of adherence to the beneficial principles of the scientific method. Otherwise, scientists have no more to offer than any other interested party. Restoration could proceed in the absence of science, i.e., restoration for its own sake.

Ecological basis for restoration

Much of what is being attempted in ecosystem restoration is uncharted territory. However, only the specifics are uncharted. In this century, the science of ecology has made significant strides with some of the most complex problems, particularly as the concepts of modern systems theory have been directed to the problems and questions. For example, our ability to assess the dynamics of fish populations and the flux of nutrients in lakes and rivers has advanced. In a report to the Great Lakes Science Advisory Board on the "Ecosystem Approach," Allen et al. (1993) emphasized three perspectives: structure, function, and landscape. A structural perspective considers the species, guilds, and communities comprising the living elements of the ecosystem. A functional perspective stresses the movements of materials within and through ecosystems, e.g., energy, nutrients, water, and sediment. A landscape perspective recognizes both spatial and temporal elements and relationships among structural and functional features. Superimposed on all these perspectives is the nested hierarchies of organization, ranging from the individual through population, assemblage, and ecosystem levels to land- and water-scapes (Table 1, after Picket et al. 1989). Each level has structural and functional properties. Structurally, species are members of guilds and guilds of communities. Functionally, energy and nutrients flow through populations, trophic levels, and whole ecosystems. Through all three perspectives we see that all interrelationships and structures are inherently dynamic. Ecosystem restoration efforts are often directed at specific elements. The ecosystem perspectives show how actions will cause wider effects that cannot be ignored.

Holling (1987) showed how the structural and functional elements of ecosystems are linked by cyclical changes in capital, the amounts of energy and nutrients sequestered in biomass, and the degrees of ecological complexity and connectance (Fig. 1, adapted from Holling 1987). Fisheries ecology has developed largely with a focus on the exploitation–conservation axis represented in Holling's diagram. Unexploited higher trophic levels accumulate biomass and complexity. Exploitation reduces the capital and often the genetic or community complexity. Holling's synthesis shows how the frame of reference for ecosystem restoration, as practised in freshwaters, needs to be expanded to include the creative destruction and mobilization phases of the cycle. Wetlands and submerged vegetation wax and wane; great storms redistribute substrates, nutrients, and species; and each event induces rejuvenation and reconstruction of habitats and communities. These systems perspectives and concepts are rarely acknowledged or considered when restoration actions are planned.

Taking a wider perspective, the application of systems thinking has expanded beyond the hard technology realm of

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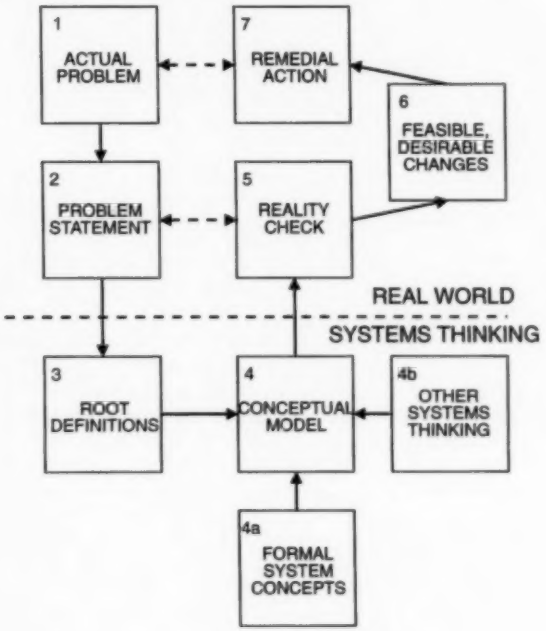
Fig. 2. An outline of Checkland's (1981) soft systems methodology, showing the separation of systems thinking from the real world and the path from recognition of the problem (1) to remedial action (7).



building bridges and launching space shuttles, into soft systems where human choices, behaviours, and interactions are central elements (Checkland 1981). Many of the approaches to aquatic ecosystem restoration are extensions of the technological approach that emerged to deal with water pollution problems in the 1960s and 1970s, treating the symptoms with waste treatment facilities instead of managing the root causes that usually result from human preference for "quick and dirty" techniques. Nowadays, ecosystem management is increasingly recognized to be a soft systems problem where human actions and preferences are essential features (Minns 1995*a*). There is no mathematical formula for a healthy ecosystem. Checkland (1981) provided a framework that organizes the analysis and decision-making process (Fig. 2). Often, when habitat alterations are being considered as part of ecosystem restoration, the approach used appears to step directly from stage 1 to 7, bypassing the intervening steps. Important steps wherein assumptions are stated and models formulated are ignored. Hence, the evaluation of options is ungrounded. Systems science guides and organizes our analysis of problems as it represents a cumulative codification of acceptable scientific methodology.

This brief overview of ecosystem science provides the context for the objective of this paper, which is to examine broadly the current state of relevant science associated with the detection of fish and ecosystem responses to habitat actions designed to restore freshwater ecosystems. We chose to sidestep the problems that beset goal setting in ecosystem management (in the sense of steward-, guardian- or trustee-ship). The basis for the choice of goals largely lays beyond the scope of science in the realm of public preference. Scientific knowledge highlights the bounds and limitations for society's goal-setting process (Minns 1995*a*). (Scientists have not emphasized the boundaries enough, perhaps, because society spurns pessimists.) Nevertheless, we have remained aware of the geographic context, the Great Lakes, and aware of the need to address a pressing concern about our collective ability to recognize and measure net gains and losses of biological productivity resulting from habitat additions, subtractions, and alterations. Our aim was to formulate assessment strategies and not to dictate exact solutions for their implementation. This review is focused primarily on freshwater fish, but we have not excluded relevant information derived from other biota, aquatic or otherwise, in keeping with our recognition of the hierarchical nature of ecosystems.

The body of this paper is divided between a review of the response detection problem and suggested approaches to the solution.

Detecting the response of fish: the problem

The problem of response detection has at least four components that need to be considered together: (1) expectations, (2) measures, (3) variability, and (4) scale. We begin with expectations, our predictive models of ecosystems, and frame expectations in measures we use as currency when describing ecosystems. When we impose a particular habitat alteration, we should predict, at least qualitatively, what the outcome will be. Shuter and Regier (1989) noted that quantitative predictions provide an important reference point for detection and interpretation of unexpected outcomes. The measures are the system properties we use to represent the ecosystem components or processes we think will change. To use the measures, we must have operational definitions and, hence, reproducible methods. The measures quantify our expectations, our hypotheses, null and alternates. Variability acts and interacts to mask the strength of signals in our measurements. Extrinsic variability derives from the inadequacies of the assessment methods that measure ecosystems. Intrinsic variability is generated in the ecosystem by the ongoing change and fluctuations in the physical (e.g., wind, currents, and temperature), chemical (e.g., weathering, erosion, and successional eutrophication), and biological (e.g., extinctions, dispersal, and invasion) phenomena that influence and determine the status of the ecosystem elements we observe. The expectations, measures, and variability are without context unless we identify scale. When spawning habitat for species *A* is increased at site *X*, spawning success is not expected to improve in all stocks of species *A*. Small increases in supply of habitats critical to a particular life stage, species, guild, or assemblage may not produce measurable changes in the chosen target. Scale may also be important when identifying the source and scope of problems; a regional problem is unlikely to be addressed adequately on a local scale and the consequences of any occurrence may take a long time to be recognized.

Expectations: explicit and implicit models

Models and hypothesis frameworks have been developed at ecosystem, assemblage, guild, population, and individual organizational levels. The identification of expectations, or alter-

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Table 2. Ecological strategy frameworks for biota describing the relationship between habitat features and life-history attributes.

Biota	Framework features	Hierarchical level	Sources
Plants	Trade-offs among competition, stress, and disturbance	Population, community	Grime 1974; Murphy et al. 1990
Invertebrates	Trade-offs between growth and mortality in relation to stress	Population	Sibly and Calow 1989
Macrobenthos	Space–time variability	Community	Townsend and Hildrew 1994
Insects	Trade-offs among productivity, disturbance, and competition	Community	Southwood 1988
Fish	Scope for activity population/community scope	Individual, population, community	Fry 1947, 1971; Neill et al. 1994
Fish	Life-history response to stress	Population	Colby 1984; Munkittrick and Dixon 1989; Shuter 1990; Schaaf et al. 1993

nate hypotheses, must be approached hierarchically (e.g., by population, community, trophic level, and ecosystem using appropriate measures) as habitat interventions do not apply exclusively to a chosen target. The initial target may be a population of a particular species, the members of a taxonomic or trophic guild, or the fish assemblage as a whole, but the responses are unlikely to be confined to the target. The array of expectations in a hierarchy provides the basis for the formulation of a framework directed to the problem of expectations in freshwater ecosystem in response to habitat interventions or alterations. Of course, if the supply of habitat is already abundant, no effect may be the expected outcome.

At the population and community levels of organization, a growing number of syntheses have concentrated consistently on the matching of life-history features to habitat attributes emphasizing the interplay of the supply of suitable or productive habitat, habitat permanence or uncertainty, and degrees of adversity (Table 2). Species respond to particular combinations of life-history capabilities, matched to and constrained by competition and habitat supply (quality and uncertainty). Guilds and communities will likewise reflect similar constraints overlain with energy flow and trophic requirements; Murphy et al. (1990) showed with frequency analysis of species' life-history strategies of submerged macrophyte that convergent "community strategies" existed in response to environmental pressures. Since ecosystem restoration usually requires habitat alterations, these explanatory frameworks should provide the basis for predicting the responses of populations and communities given an appreciation of supply and scale.

As Table 2 also shows, the number of frameworks applicable to fish is growing. Colby (1984) and later Munkittrick and Dixon (1989) showed how life-history attributes, such as size at maturity, fecundity, and survival, respond to exploitation and changes in physical and chemical habitats. Shuter (1990), Schaaf et al. (1993), and others have begun to examine these response frameworks in the context of population dynamics. Shuter (1990) showed the consequences of "bottlenecks" at different life stages to population structure and persistence. Schaaf et al. (1993) showed how small changes in habitat supply can generate large changes in population size when habitat bottlenecks are the target of degradation or restoration. Ecosystem restoration activities must be directed to the habitat bottlenecks but not without consideration of other limitations that may stop a population or community realizing the potential of an particular action. Many bottlenecks may be present and interlinked although only one can be limiting at any point (Kozlowski 1985, 1986). Society tends to mistakenly think that relieving immediate bottlenecks will provide a cure-all.

When restoration actions are applied, many questions need to be answered if we are to confidently select actions. Decision-makers are often unready to confront this problem. If fish species *X*, targeted for restoration, increases, have the abundances of species *Y* and *Z* changed? Are the increases or decreases illusory and only evidence of redistribution? Has the space–time pattern of habitat usage changed? Have other ecosystem elements, such as benthos, zooplankton, or macrophytes, responded? Decision-makers try to narrow the scope of assessments and are often unready to confront the wider questions.

Syntheses of response expectations are more advanced at the population level compared to guild and community levels. Hence it is not surprising that fisheries ecologists and anglers tend to focus on population level phenomena. However, evaluation of responses to habitat manipulation, alterations, and interventions should probably begin at the guild or community levels. Populations inevitably interact and share resources. A community-level approach represents a considerable intellectual challenge as it is very difficult to conceptualize the interlinked dynamics of more than two or three entities. However, in the evaluation of habitat alterations in real ecosystems, limiting ourselves to the formulation of hypotheses about single entities is probably unproductive.

Habitat alterations might be expected to invoke four types of community and ecosystem response: (1) total fish biomass and production changes, (2) fish assemblage composition (species richness, the distribution of biomass, and production by species) is altered, (3) the distribution of some or all elements of the fish assemblage in time and (or) space is altered, and (4) a response occurs in the non-fish biotic elements of the target ecosystem. The combination of presence or absence of these four responses generates sixteen possible response patterns, ranging from no response to every element of the ecosystem responding (Table 3). To understand the effects of habitat interventions, measurements that assess the components of the response are needed.

Among the 16 combinations (Table 3), the first, where nothing responds, is the null hypothesis and the other 15 represent alternate hypotheses. Since the focus of this discussion is the restoration of fish communities, non-fish responses are of less immediate interest and the number of alternate hypotheses may be reduced to a more manageable eight. (A full examination of the potential consequences in an ecosystem of any action is a challenge and new ways of tackling the problem

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Table 3. Hypotheses matrix for freshwater fish assemblage in response to a habitat and other ecosystem alterations.

		Change in total fish biomass and production?			
		No		Yes	
		Change in non-fish biota?		Change in non-fish biota?	
Change in fish assemblage composition?	Change in fish distribution patterns?	No	Yes	No	Yes
No	No	H_O	I	IIA	IIB
	Yes	IIIA	IIIB	IVA	IVB
Yes	No	VA	VB	VIA	VIB
	Yes	VIIA	VIIB	VIIIA	VIIIB

Note: Four response indicators can generate 16 outcomes.

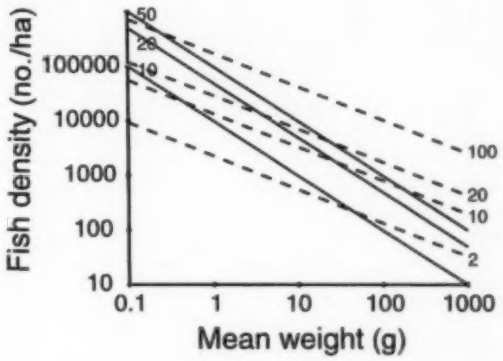
Table 4. An indication of the range of measures available for assessing fish response at different organizational levels.

Level	Measures
Individual	Size, growth, condition factor, health, contaminant level, maturity, fecundity
Population	Presence–absence, CPUE, age structure, abundance/density, biomass, production, space–time distribution, size structure
Assemblage	Species richness, biomass, productivity, composition (size, trophic, species), distribution (interspecies)

of hypothesis formulation are needed.) Alternative I implies that the intervention was mistargeted as fish did not respond (Table 3). Alternative II implies a proportional response among all members of the fish community without impacts on composition or distribution, an unlikely event. Alternative III has the distribution changed but nothing else. This response has been hypothesized in conjunction with the construction of reefs and other fish structures. It is hard to argue that restoration has occurred in this instance. Alternative VII seems more likely as restoration alters the relative supplies of various habitat types and hence alters distribution and composition. Alternative IV is a preferred response to restoration; biomass and production changes along with distribution. This is unlikely to occur without compositional changes. Alternative V is also unlikely; composition changes in the absence of biomass, production, and distributional responses. The alternate hypotheses might be ordered by their likelihood: VII > VIII > VI > V > III > IV > II. Unless actions are directed to increasing ecosystem productivity, such as by increasing nutrients, increased biomass and production is an unlikely outcome. Changes in physical habitat most likely produce changes in distribution and composition; VII and VIII are the most likely.

At the next lower hierarchical level, habitat interventions can directly affect biomass and production in a species population. However, in the management of whole fish assemblages or ecosystems, it is important to know if other biotic components increased as result. Increase in one species is unlikely to be sustained without other biota being negatively affected. The type of response detected will depend on the form of the habitat alteration.

Fig. 3. Biomass ($kg \cdot ha^{-1}$, solid lines) and production ($kg \cdot ha^{-1} \cdot year^{-1}$, broken lines) thinning curves, or isolines, superimposed on the relationship between mean weight and population density for freshwater fish communities (after Randall et al. 1995).



Measures and definitions

There is a well-established array of measures and indices for fish at the individual, population, and assemblage levels of organization (Table 4). Karr's index of biotic integrity (IBI) is an example of a community index developed for stream fishes, which merges measures and has been applied widely in the United States and Canada (Fausch et al. 1990). Minns et al. (1994) have applied the IBI approach to fish assemblages in the nearshore waters of the Great Lakes. In choosing measures, care is required and some redundancy is necessary to allow scope for unexpected interactions and response patterns to be detected.

For example, density per se cannot be taken as a sole indicator of habitat quality. In fish populations and assemblages, density needs to be examined in conjunction with mean size (Boudreau and Dickie 1992; Randall et al. 1995). Taken together, density and mean weight are indicators of both biomass and production (Fig. 3). Biomass isolines (solid lines in Fig. 3) are steeper than production ones (broken lines), and changes in density without knowledge of size may be misleading. As Van Horne (1983) pointed out, comparisons of habitat quality must involve measurement of some aspect of fitness. He noted three ways wherein density can be a misleading indicator of

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Fig. 4. Average number of fish species missed per year in relation to total fish species richness for a set of lakes in the Algoma region of Ontario (J.R.M. Kelso, unpublished data; 20 lakes each sampled in 3–5 years).

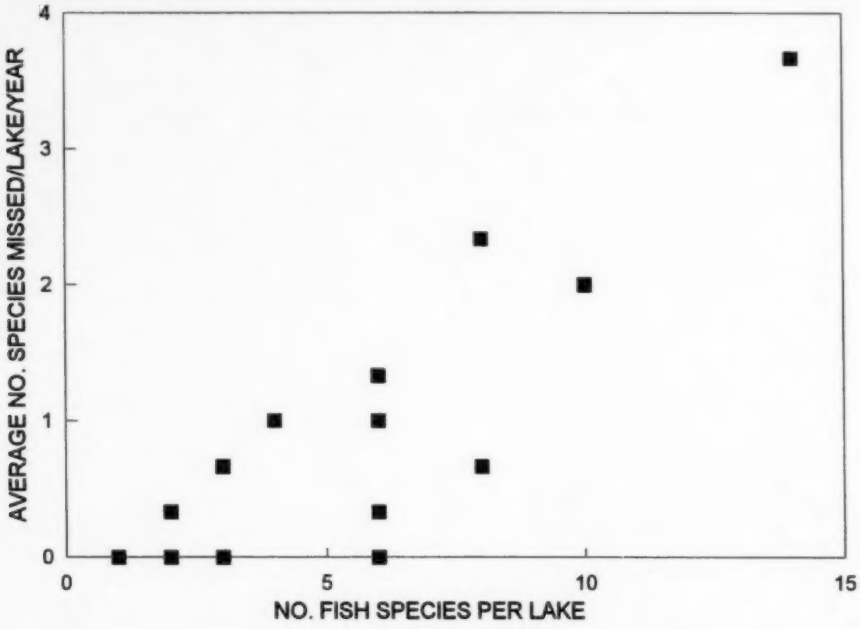

Table 5. Comparison of common, those contributing to 95% of abundance, and rare (contributing <5% to abundance) macroinvertebrate species in four lakes in the Turkey Lakes watershed, Ontario, in 1988 and 1989.

	Batchawana Lake							
	N. Basin		S. Basin		Wishart Lake		Little Turkey Lake	
Category	1988	1989	1988	1989	1988	1989	1988	1989
No. of species comprising 95% of abundance	37	21	37	24	43	38	56	21
Common taxa losses		2		8		9		23
Common taxa gains		1		1		5		2
No. of rare taxa	59	60	35	44	45	30	62	44
Rare taxa losses		25		21		29		40
Rare taxa gains		22		20		13		14

habitat quality for common species: (1) social interactions in seasonal habitats, (2) high fecundity in the presence of temporary habitat favourability, and (3) generalist species exploiting patchy environments.

Variability

Variability of structure and function in space and time will act to confound efforts to detect ecosystem responses to restoration activities. However, several consistent patterns of variability have emerged that can be used to guide the design of response assessment programs: (1) variance (V) is strongly related to the mean (M), e.g., "Taylor's Power Law" where $V = aM^b$ (Taylor 1961). The exponent b is generally about 1.5 in aquatic biota (Downing and Downing 1992); (2) the power law holds for both temporal and spatial variability (Taylor and Woiwod 1980); (3) spatial variability is generally greater than temporal (Taylor and Woiwod 1982 for insect and bird populations; Elliott 1992 for sea-trout catches in the United Kingdom); and (4) variability increases with the temporal and spatial scale (Pimm and Redfearn 1988; Bell et al. 1993). Habitat is usually a primary cause of population variability (Eadie and Keast 1984). (5) Temporal and spatial habitat variabilities interact, affecting our ability to detect changes (McArdle et al. 1990) while generating population variability (Fahrig 1992). Temporal variability adversely affects the detection of changes due to actions and alterations (Power 1993). For example, the changes to and increased variability in global climate patterns may already be confounding efforts to detect responses to localized actions.

Specific aquatic ecosystem instances highlight and emphasize the significance of the patterns of variability and the difficulties faced. Repetitive surveys of fish populations in lakes to detect community structure, abundance, and mass (Green 1986; Fig. 4) indicate either significant variability in the property or lack of reproducibility in the method (Figs. 4 and 5). This dichotomy in understanding variability in ecosystems ap-

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Fig. 5. Annual brook trout abundance, biomass, and production for Lawrence Creek, Wisconsin, 1960–1970 (after Hunt 1974).

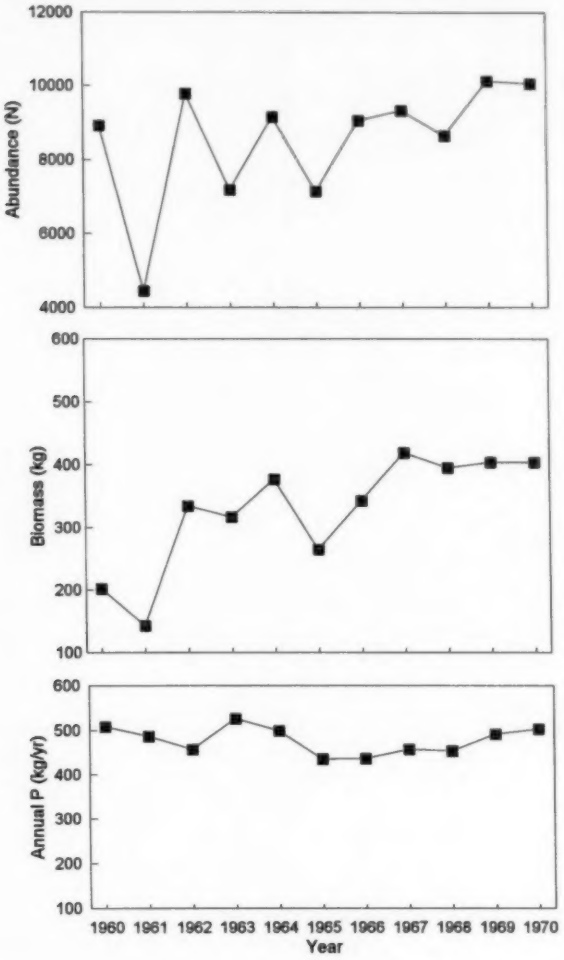
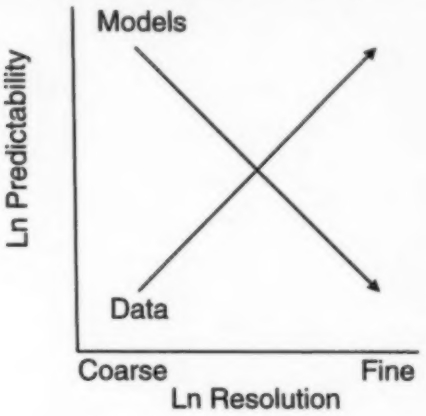


Fig. 6. Relationship between predictability and resolution for models and data (after Costanza and Maxwell 1994).



plies to fish (Figs. 4 and 5), macroinvertebrate communities (Table 5), and probably most environmental and biotic characteristics of systems. Increasing sample size does little to remove variability in this type of data because similar intensive (combined application of multiple gill nets, trap nets, and minnow traps set repetitively) effort applied over 3–5 years (Fig. 4) and data for more than 60 lakes contained appreciable variability.

Conversely, ecosystem properties such as biomass and production may be intrinsically stable with limited variability (Kelso and Ward 1972; Hunt 1974; Kelso and Bagenal 1977; Kelso and Ward 1977; Dickie et al. 1987; Kelso 1988; Downing et al. 1990; Kelso and Johnson 1991; Downing and Plante 1993; Randall et al. 1995). Hunt (1974) in an excellent study in Lawrence Creek showed that annual production of brook charr remained remarkably stable (coefficient of variation (CV) = 6%) over 10 years despite stream alterations while age class structure changed and, abundance and biomass showed more variability (CVs of 20 and 28%; Fig. 5). Data for entire communities are scarce, restricted in number and latitude, and usually provide only 2–3 years of data, but whole lake biomass and production appeared to vary little (Kelso and Ward 1972; Kelso 1988).

If these examples realistically reflect our ability to measure assemblage and species population characteristics, and ecosystem attributes, it may be that effects of extrinsic and intrinsic variability are greatest when attempting to detect repeated patterns and relationships of properties such as species richness, relative abundance, and catch per unit of effort and least when examining ecosystem properties such as whole lake biomass and production.

Scale as context

Scale is important as a context for understanding and detecting responses to habitat alterations in three ways. First, there is the nested hierarchy of spatial and temporal scales at which (1) ecosystems operate, (2) human interventions impacts tend to occur, and (3) our assessment efforts are carried out. The sequence from 1 to 2 grades generally from large to small spatially and from long to short temporally. The reference contexts for assessing impacts are often set at too fine a scale. Costanza and Maxwell (1994) have pointed to the scaling mismatch of model and data predictabilities (Fig. 6). Models that invariably represent generalizations are more predictive at coarser resolutions, while data is less variable at finer resolutions. Choosing finer scales of resolution for response detection increases the likelihood that we will conclude that the models failed. Uncertainty is then often used, somewhat perversely, to justify proceeding with human use development while retarding the application of uncertain restorative actions.

The understanding of a landscape or waterscape perspective of ecosystems has been expanding rapidly (Clark 1985; Urban et al. 1987; Holling 1992; Horne and Schneider 1994). Holling (1992) put forward a striking model where relatively few biotic and abiotic processes create the main spatiotemporal structure in ecosystems. At the population level, here loosely interpreted for freshwater fish, a nested hierarchy of space–time domains describes the way populations exploit

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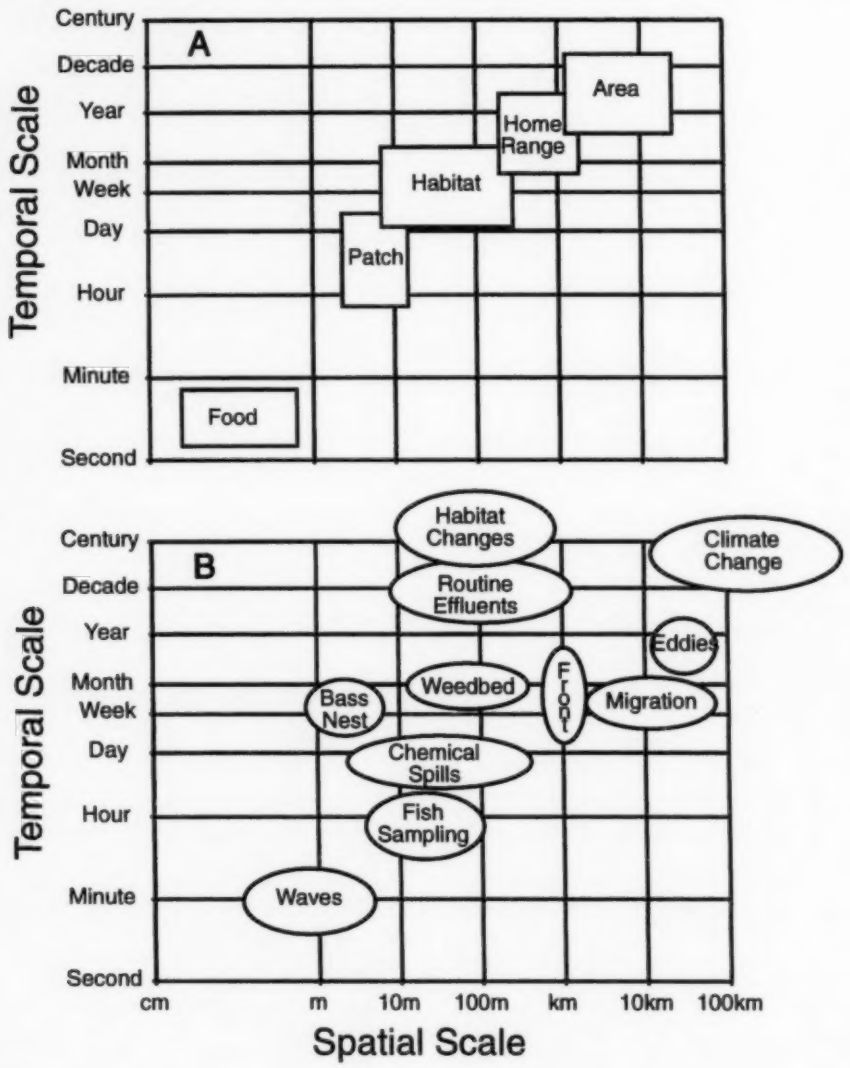
Fig. 7. Diagrams illustrating the spatial and temporal scales of (A) fish population use of habitat for life-history requirements (adapted from Holling 1992) and (B) events and activities impinging on fish populations (after Clark 1985; Urban et al. 1987; Holling 1992; Horne and Schneider 1994).



space and time (Fig. 7A). Home range depends on the size of the fish (Minns 1995*b*) and population area depends on population size and lifestyle. Superimposed on this population scale template, various events and phenomena occur and influence the success of the population (Fig. 7B). The scale of habitat interventions, e.g., spawning habitat change, are localized while events such as phosphorus and contaminant loading are systemwide. Our attempts to measure ecosystem response are on a small scale compared with the system being modified.

In the Great Lakes, habitat alterations are often proposed with little knowledge or consideration of the spatial scale to which the target species populations are tied. Recent work (Minns 1995*b*) provides some indication of the spatial scale of home range for individual freshwater fish. Home range is largely determined by fish size, reflecting the role of energy consumption in determining use of habitat space and comparable with those seen for similar weight animals in terrestrial ecosystems. Holling's (1992) analysis of nested hierarchies of paired spatial and temporal scales indicates how population scales might relate to individual ones. For fish ranging in size from 100 to 5000 g, home ranges are typically 1–10 ha in lakes and about 0.04–0.4 ha in rivers. Migration ranges can be much larger. Population or metapopulation ranges (areas in Holling's terminology) for freshwater fish in lakes might be expected to be on the order of 10–1000 ha, again depending on fish size. Thus, for dominant large predators, which are

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often the preferred target for ecosystem restoration efforts in lakes, large areas are involved in the production and sustainability of their populations. Hence, habitat alterations on the scale of tens to hundreds of square metres might not be expected to greatly influence population size or performance unless the site affected exerts a critical influence, e.g., restores the only spawning site within the population range.

Approaches to solutions

Having pointed to the difficulties associated with detecting biotic responses to habitat alterations, we must be prepared to offer some approaches to their solution. There are four areas where progress should be sought: experimentation, science, ecosystem management, and coordination.

Experiments, experiments, experiments

In a review of current trends in conservation biology, Caughley (1994) states "Management actions are experiments and should be run as experiments according to the standard rules of experimental design. Otherwise nothing is learned from them." He lists five steps necessary to identifying and fixing problems in declining populations, steps that are applicable to habitat interventions: (1) Use science to learn why the population declined and what was the causative agent. Don't assume the answer is known. (2) Remove or offset the causative agent. (3) Use a probe to confirm the deduction. (4) If right, restock by translocation, or, if very low and (or) stock unique, breed. (5) Monitor reestablishment.

Science is required in all steps. In freshwater fisheries in the Great Lakes, there is little evidence that scientific methods are routinely used to guide the selection of habitat alterations. Those advocating habitat alterations need to acknowledge that many of the interventions are unproven and that the actions must be considered experimental. If an action is experimental, Caughley's dictum should apply. Going further, Underwood (1995) has recommended that ecologists undertake coordinated studies of management decision-making and its results.

The specification of statistical designs for assessing environmental impacts has been advancing rapidly. Green (1979) described BACI (Before/After-Control/Impact) designs. BACI has been both criticized and modified (cf. Underwood 1991 for the history). Major issues have been (1) replication and controls (Hurlbert 1984), (2) the characterization of perturbations as pulse or press (Bender et al. 1984), and (3) the need to increase the statistical power of designs (Fairweather 1991). Gradually an improved set of criteria have emerged, described by Underwood (1991, 1993) as "Beyond BACI."

Underwood (1991, 1993) has summarized the main features of a "Beyond BACI" experiment: (1) treatments and controls need to be sampled several times before and after application of the treatment; (2) each sampling requires several replicates; and (3) where a single treatment site is involved, several spatial controls will be required. These simple, minimum requirements are rarely met in habitat restoration experiments. If we consider a single treatment, the bare minimum for a valid experiment would appear to be: 1 treatment plus 2 controls, 3 samplings before and after, and 2 replicate samples at each sampling, giving a total of 36 samples. In situations where funding for intervention is the driving force, habitat restorers will have difficulty defending the expenditure of two thirds of their effort at sites other than the one where the habitat alteration occurs and only one sixth of their sampling effort at the treatment site after treatment is implemented.

Judging by many extant instances, the myth that the impact of habitat alterations can be assessed merely by regularly monitoring the treatment site before and after the alteration has great resilience and persistence. If the difficulties of sampling enough to ensure reliable detection levels are taken into account, most likely the overall sample size will have to increase, via more spatial controls, more samplings before and after, and more replicates. Thus, level of effort required to achieve statistical rigor may be formidable. Hence, we must be careful to identify which habitat alteration actions we need to test. The requirements of "Beyond BACI" address the distributional response axis in the hypotheses matrix (Table 3).

Science, science, and science

As we indicated above, science is often absent or neglected when actions to restore ecosystems are being planned. Often the science is not used because the objects of ecosystem restoration are poorly defined. Vague notions of improving ecosystems are metaphysical. Rationales for habitat alterations are often anecdotal or nonexistent. Science involves the construction and testing of predictive models. Application of science to restoration requires that predictions be made before the actions proceed. Much of the necessary science is, in fact, available.

The fields of systems, freshwater, and fisheries ecology are well developed with an array of established concepts and empirical knowledge. Besides that immediately applicable science, there needs to be greater cross-fertilization with other, often nonaquatic, fields such as terrestrial ecology, conservation biology, and physical geography. Robust concepts abound in these fields and are often applicable in aquatic ecosystems. In terrestrial ecology, gap analysis is emerging as a major approach to landscape analysis directed to conservation of biodiversity (Scott et al. 1993). Caughley's (1994) review of conservation biology points to the growing role of population viability analyses in setting numerical targets. Where the necessary science is not available, experiments can fill the gaps.

Ecosystem management

Too often society is assumed to have agreed about the objectives of ecosystem management. Narrowly defined ecosystem management is unlikely to succeed. Grumbine (1994) recently provided an overview of what factors contribute to the concept of ecosystem management. He identified a general goal of maintaining ecological integrity in the long term or sustaining healthy ecosystems. Five specific goals are given: viable populations, representative ecosystems, ecological processes, evolutionary potential, and, after the first four have been attained, accommodating human uses. Grumbine's reasoning for the low priority of human use is simple. Although humans might wish to place their use preferences first, sustained ecological integrity must take precedence if any human use options are to be retained. Tonn (1986) suggested that the long-term view should be of the order of 500 years. Rapport (1989), Minns (1995*a*), and others, have suggested that a more holistic, integrative perspective is needed, analogous to a linked mind–body view of human health. Methods enabling this type

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of approach are emerging, e.g., the AMOEBA-approach of Brink et al. (1991). This view of ecosystem management is broader in scope and longer term than current practice in most ecosystem restoration efforts, including those in the Great Lakes.

Coordination, consultation, and cooperation

In an era when staff and budgets of many environmental agencies are being cut back, finding new ways to produce the science needed as a basis for rational ecosystem management must be sought. Habitat alterations, good and bad, will proceed regardless of the science available and the implementation of assessments. Scientists must seek ways to create science-added value for all projects. Walters and Holling (1990) and others have suggested ways in which management and science can become a partnership where every action is an opportunity to increase knowledge even if the action occurs in a manner incompatible with conventional hypothesis testing. This learning by doing still requires that careful observations be made before and after the action occurs. Walters and Holling urge the use of active rather than passive adaptation; successive policy choices and actions are selected with a view to achieving the desired effects (short term) and learning if alternative models were correct (long term). They also urge approaches that recognize the occurrence and persistence of uncertainty.

Hinch (1991) called on fisheries scientists to enter into regional partnerships to allow complex issues to be addressed by cooperating groups. Resource management issues are rarely assessable by a few individuals working in a one or a few locations. There are several examples of coordinated research–assessment networks. As part of Canadian studies of the impacts of acidic deposition, a series of calibrated watersheds was established across the affected regions (Jeffries et al. 1988). That network is proving invaluable in other regional issues such as long-range transport of organic contaminants and climate change. In Ontario, the Ministry of Natural Resources laid the groundwork for a network of fisheries assessment units covering regional representative groupings of freshwater ecosystems. Results are being used to synthesize knowledge of key fish species and to formulate management and conservation strategies. This kind of coordinated effort is evolving in the habitat restoration arena. On the Great Lakes, there is a binational commitment to restoring ecosystem health, and similar but largely uncoordinated actions are occurring at many of the 43 Areas of Concern. In Lake Superior, habitat restoration efforts are planned and implemented by a single group. Such efforts can provide the basis for cooperative assessment experiments, evaluating the usefulness of various types of habitat alterations, e.g., reef creation, wetland rejuvenation and restoration, spawning habitats, etc. Also on the Great Lakes, the binational commitment extends to the development of lakewide ecosystem management plans (LaMPs). Habitat restoration and conservation are emerging as major factors in the campaign to restore ecosystem integrity and further opportunities for coordinated assessment activities are appearing. The Great Lakes Fisheries Commission also provides the means for enhanced cooperation and collaboration in the experimental assessment of habitat actions, building on the fishery management coordination efforts of the lake committees.

Concluding comments

In this paper, we do not claim to have written anything particularly new or insightful. Rather, we have tried to provide a timely reminder that scientists must do science when they participate in efforts to restore ecosystems. In simple terms, this means that decision-makers must affirm that management actions are experiments and provide an opportunity to learn. Also, ecologists and decision-makers must not ignore or forget the large body of knowledge and understanding already accumulated. This is true both within the immediate field of fisheries ecology and beyond in terrestrial ecology, landscape ecology, geography, etc. Scientists tend to become narrow in their outlook and expertise. This tendency is alarming when we see that the ecosystem management challenges are holistic requiring the integration and synthesis of seemingly disparate pieces of science. It is how society uses its science that seems to be an increasing problem.

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Use of historical information for conservation and restoration of Great Lakes aquatic habitat

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Abstract: We provide a rationale and methodological overview for historical (retrospective) study of Great Lakes aquatic habitats and biota. Historical information has significant potential to direct aquatic habitat management in the Great Lakes, particularly in setting restoration goals. Although the use of historical information has been opportunistic (it is limited by the preservation of information in specific forms) and generally of low resolution (it is generally semiquantitative at best), the products of these analyses have been compelling (they have changed the attitudes and expectations of people) and surprising (many of the conclusions of historical analysis were not predictable from other sources).

Résumé : Nous présentons une justification et un aperçu méthodologique pour l'étude historique (rétrospective) des habitats aquatiques et du biote des Grands Lacs. Les informations historiques présentent un grand intérêt parce qu'elles peuvent faciliter la gestion de l'habitat aquatique des Grands Lacs, notamment pour ce qui est de la définition d'objectifs de restauration. Bien que l'utilisation des informations historiques soit de type opportuniste (elle est limitée du fait que l'information est préservée dans des formats particuliers) et généralement à faible résolution (au mieux, elle n'est généralement que semi-quantitative), les résultats de ces analyses ont été convaincants (ils ont contribué à changer certaines attitudes et attentes) et surprenants (bon nombre des conclusions des analyses historiques n'étaient pas prévisibles à partir d'autres sources).
[Traduit par la Rédaction]

Introduction

There is little doubt that retrospective study of Great Lakes aquatic ecosystems, including human uses and abuses, can underpin future efforts to conserve and restore aquatic habitats (National Research Council 1992; Doppelt et al. 1993; Montgomery et al. 1995; Nielsen 1995). A key use of historical information is to describe pre-industrial ecosystems in support of attempts to restore beneficial features of degraded ecosystems. Another key use of historical information is to help calibrate present expectations regarding the productivity, diversity, and stability of the natural systems upon which humans depend. Retrospection is also the most immediate empirical test of "environmental sustainability."

This contribution provides a rationale and methodological overview for historical or retrospective analysis of Great Lakes aquatic habitats and biota and attempts to extract and synthesize useful generalizations and patterns from the HabCARES proceedings, regarding historical analysis. In the context that we use the term, historical analysis includes systematic attempts to obtain information about historical or prehistorical ecosystem states or about the human activities influencing those past states. Analysis of long-term data collected with strategic foresight (e.g., Young et al. 1996; Casselman and Lewis 1996), should probably not be called historical analysis. This can be contrasted with directed but opportunistic analysis of preserved or recorded information from the past (e.g., Bray 1996; Kelso et al. 1996). However, we may refer to either type of analysis to illustrate a concept. Our synthesis focused on the Great Lakes region, but we used information and analogies from other regions and ecosystems where appropriate.

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Why is it important to consider historical information?

Historical information is important in ecology for many of the reasons it is important in other areas of human interest, such as culture or earth sciences.

(1) Those who ignore history are doomed to repeat the worst of it (Wil. E. Coyote)

The foremost task in conserving and restoring aquatic habitat is not to directly repair habitat features (although that can be important) but to eliminate or modify the human activities that destroy habitat or that prevent natural recovery following disturbance. Knowing past actions that destroyed habitat can help alter human behaviour so that mistakes are not repeated. For these reasons, historical descriptions of species composition, habitat features, and landscapes can be important elements of efforts to preserve remaining habitats, and restore degraded ones (e.g., White 1996; Kelso et al. 1996; Kelso and Cullis 1996; Koonce et al. 1996; Evans et al. 1996; Whillans 1996; Busch 1996).

History can also help illuminate the patterns of human activity, attitudes, beliefs, and perceptions that led to habitat damage. Technological, economic, social, political, cultural, and religious motivations for human endeavour, as revealed in history, can be used to guide future human action in directions that are less harmful ecologically. The character and expression of each of these aspects is always changing. Retrospective analysis can contribute to management and prediction of such change (Evans et. al. 1996; White 1996).

(2) Historical information is frequently required during the specification of targets for ecosystem restoration

As ecosystem degradation becomes recognized, and remediation or restoration is planned and implemented, it is important to have information about the state of ecosystems before humans degraded them. Unless the direction of habitat restoration is derived exclusively from pragmatic, aesthetic, or theoretical considerations, a historical image of the habitat is necessary when setting goals for restoration planning (e.g., Hansen et al. 1995).

(3) Historical information can be used to modify values and beliefs as they relate to habitat

Science has an important role to play in the development of biologically sensitive expectations of natural ecosystems. Even though resource managers may have clear and accurate perceptions of major human activities that are destroying fish habitat and even though they may know what should be done to rectify the problems, they often find it hard to convince people to undertake the needed reforms. Informing stakeholders about historical trends of habitat and biotic decline, and associated trends in human activity, may help to raise their general awareness of the problems and their solutions. Chronological narratives are relatively easy to follow and relate to personal situations.

(4) By its very nature, information about natural ecosystem processes needs to be interpreted in a context that is long term and retrospective

Geologists and geomorphologists have long recognized that one's temporal frame of reference affects conclusions about cause, effect, and significance in natural systems. For example, depending on the interval of observation, channel profile and channel pattern in rivers can be seen as either a cause of habitat diversity or an effect of local geology and physiography (Schum and Lichty 1965). Many important ecological phenomena related to habitat structure arise and evolve as a result of subtle, complex, and interacting physical and biological processes acting over periods ranging from years to centuries, only to be punctuated by extreme, rare, or unique reset events, such as storms, earthquakes, or volcanoes, or climate change. Many key features of contemporary North American aquatic ecosystems are a direct result of such processes. Moreover, scientists such as Sale (1978) have reasoned that the occupation by fish of habitats after such events also has an important stochastic element.

(5) Humans are not very good at perceiving slow processes or rare events without the help of scientists or historians

Perceptions of natural systems are strongly affected by individuals' assumptions about "normality," regarding both ecosystem state and ecosystem dynamics. Informal knowledge can be affected by the vagaries of human memory, leading individuals to remember their world through a moving window extending backwards in time for some period that is less than their life-span. Such a short temporal frame of reference will obscure or minimize the importance of infrequent natural disturbances that reorganize and reset natural systems, and will also appear to "freeze" very slow processes that do not change perceptibly during the period of observation. Systematic retrospective analysis of ecological information, coupled with long-term study of contemporary systems, is perhaps the best means of avoiding these problems. Humans are not very effective at recognizing phenomena that take place at scales significantly larger or smaller than those readily perceived through their five senses. Understanding landscape-scale or microscopic processes, like understanding slow, rare, or very fast processes, is generally not achieved without the systematic collection and interpretation of information that is typically undertaken in a scientific or historical context.

(6) In culture, religion, and science, humans have often preferred to seek out and preserve stability in the natural world and to filter human perceptions through models grounded on stability or steady-state dynamics (Prigogine 1980)

Such attitudes have led to the suppression and undervaluing of natural systems' abilities to create and regulate their structure and function, as well as to repair themselves when they are damaged. Retrospective analysis and long-term study are slowly reducing scientific emphasis on "stability" as an ecological norm and replacing it in some cases with models incorporating surprise or catastrophe as normal elements (Brooks 1986; Holling 1986).

(7) Human perceptions and expectations are influenced by the highly modified and simplified state of most contemporary landscapes

As a result, the importance of complexity in natural systems is frequently underestimated (Kay 1993). Ironically, there has

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Table 1. Examples of retrospective studies on Great Lakes aquatic habitats. Where the type of retrospective technique has not been specified in parentheses under "General topic," the study was based on numerical data and/or qualitative observations.

Author	Date	General topic	Period
Milner	1874	Fish abundance, exploitation levels, Great Lakes	1870–1874
Smiley	1882	Fish abundance, exploitation levels, Great Lakes	1870–1880
Smith and Snell	1891	Fish abundance, exploitation levels, Great Lakes	1870–1890
Wright	1892	Natural history, Great Lakes	1870–1891
Wilmot and Harris	1893	Fish, exploitation, habitat degradation, Great Lakes	1860–1892
Langlois	1941	Fish abundance, habitat degradation, western Lake Erie	1880–1940
Huntsman	1944	Atlantic salmon, exploitation, habitat changes, Lake Ontario	1870–1900
van Oosten	1948	Fish abundance, exploitation, Lake Erie	1913–1945
Beeton	1969	Fish and forage abundance, water quality, Great Lakes	1850–1968
Regier et al.	1969	Fish, exploitation, habitat changes, western Lake Erie	1900–1968
Berst and Spangler	1973	Fish, exploitation, habitat changes, Great Lakes	1880–1970
Christie	1973	Fish, exploitation, habitat changes, Lake Ontario	1800–1970
Hartman	1973	Fish, exploitation, habitat changes, Lake Erie	1880–1970
Lawrie and Raher	1973	Fish, exploitation, habitat changes, Lake Erie	1900–1970
Wells and McLain	1973	Fish, exploitation, habitat changes, Lake Michigan	1850–1970
Regier	1979	Overview of human-caused changes to Great Lakes fish communities	1880–1978
Whillans	1979	Fish, exploitation, habitat changes, Lake Erie and Lake Ontario bays	1800–1975
Warwick	1980	Habitat change: palaeolimnology, water quality, land use, sedimentation, chironomid fossils, Bay of Quinte, Lake Ontario (sediment cores)	800 BC –1972
Goodier	1981	Fish, habitat change, north shore Lake Superior	1870–1970
Trautman	1981	Fish, habitat change, Ohio	1880–1980
Harris and Vollenweider	1982	Habitat change, Lake Erie (sediment cores)	1800–1980
Whillans	1982	Wetlands change, north shore Lake Ontario (maps)	1790–1980
Holmes and Whillans	1984	Fish, habitat, Hamilton Bay, Lake Ontario	1790–1980
Lyon and Drobney	1984	Habitat change, Lake michigan (aerial photos)	1940–1980
Martin	1984	Recent land use effects on fishes of Credit River, Lake Ontario	1950–1983
Martin	1985	Land use and fish associations of Don River, Lake Ontario	1800–1980
Whillans	1985	Fish, habitat, exploitation, Long Point, Lake Erie (sediment cores, interviews, aerial photos)	1920–1979
Egerton	1985, 1989	Productivity, exploitation, habitat change, Lakes Erie, Michigan, Huron	1870–1980
Steedman	1986	Sequence of burial of small streams in urban Toronto, north shore Lake Ontario (maps)	1780–1920
Charlton	1987	Habitat change, Lake Erie (sediment cores)	1920–1985
Hall and Ide	1987	Habitat change, Lake Ontario headwaters (re-survey)	1937–1985
MacCallum	1989, 1994	Fish, habitat, history of fish community, Nipigon River, Lake Superior (interviews, diaries)	1837–1989
Wichert	1991, 1994*a*, *b*	Fish habitat, Toronto-area streams, north shore Lake Ontario (maps)	1948–1985
Bray	1993	Fish habitat, St. Marys River, Lake Superior, Lake Huron (model)	1790–1990
Mills et al	1994	History and mechanisms of exotic species introductions to Great Lakes	1810–1990
Kelso et al	1996	Analysis of historical commercial fish yields, in context of habitat degradation	1870–1990

also been a tendency to underestimate the pervasive and ancient effects of human activity on seemingly "wild" landscapes. This is another manifestation of the moving window of historical perception and of the fact that many so-called "natural" features were already seriously altered by human activity before they were monitored systematically (Moss 1980; Harris and Matthews 1987). Even relatively recent industrial effects on natural systems are poorly understood, as has been documented by Sedell and Luchessa (1981) and Doppelt et al. (1993) regarding splash-damming and channelization of North American rivers in the 1800s and by Whillans (1979) regarding "stone hooking" in the littoral zone of the lower Great Lakes.

(8) The present is the "history of the future"

Limitations of the current historical record result in ecological uncertainty and risky decisions. Ecology is an evolving set of hypotheses about interactions among biophysical components in ecosystems; as information improves in resolution and accuracy, hypotheses are modified or rejected. Agencies and institutions need historical guidance to complete this cycle and must take steps to ensure that important data are collected, managed, and archived according to appropriate protocols (Shepanek 1994).

What do we know about the history of Great Lakes aquatic habitats?

General histories abound for the Great Lakes region. The references listed in Table 1 are intended to provide a selective introduction to the historical material and techniques available to researchers and managers interested in historical states of

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Table 2. Potential applicability of various information sources for retrospective analysis.

	Ecosystem feature[a]							
	Physical							
	Shoreline	Bathymetry	Particle size	Channel form	Water levels	Discharge	Currents	Temperature
Accumulators								
Biota	—	—	—	—	L	—	—	M
Sediment	—	—	H	—	H	L	—	M
Residues								
Microfossils	—	—	L	—	L	L	—	L
Macrofossils	—	—	L	—	H	L	—	H
Museum references	—	—	—	—	L	L	—	L
Landscape pattern	—	—	—	—	H	L	—	—
Inorganic	—	—	H	—	L	—	—	—
Replicates								
Air photos	H	L	L	H	M	L	—	—
Other remote images	M	L	L	M	L	—	—	—
Art and photographs	L	—	L	L	L	L	—	—
Historic observations	L	L	L	L	L	L	L	L
Historic data	L	L	L	L	H	H	M	M
Oral histories	L	L	L	L	L	L	L	L
Maps	M	M	L	M	L	—	M	M

[a] H, high; M, medium; L, low.

[b] Large, regional scale; medium, drainage basin scale; small, river reach or shoreline segment scale.

[c] Short, 100 yr; medium, 101–300 yr; long, >300 yr.

Great Lakes aquatic habitats. These materials range from reports of resource managers, to historical, narrative overviews of natural or cultural history, to recent quantitative analyses of archived information.

The first prominent historical assessments in the Great Lakes basin date back to the lake 1800s when fisheries regulators in Canada and the United States attempted to determine reasons for the widespread decline of fish harvests (Milner 1874; Smiley 1882; Smith and Snell 1891; Wilmot and Harris 1893; Wright 1892). Exploitation was emphasized. Scientists picked up this theme periodically throughout the first half of the 20th century (Langlois 1941; van Oosten 1948). However, it was not until the 1960s that habitat received significant attention. Scientists such as Regier et al. (1969) and Beeton (1969) paved the way for systematic historical assessments of environmental influences on fish in the Great Lakes (Loftus and Regier 1972).

This body of information documents the well-known pattern of rapidly increasing, destructive exploitation of the region's natural resources, including stream and nearshore aquatic habitat, fish populations, and water quality, from the time of European settlement of the region until about the middle of the 20th century (Whillans and Berkes 1986). In relatively recent years, this has been followed by relaxation or elimination of many of the most acute abuses, particularly those related to organic pollution and commercial overharvest of fish. The trends of ecosystem degradation were strongly associated with human population density and industrial activity, such that the upper Great Lakes were relatively less impacted than the lower Great Lakes (Botts and Krushelnicki 1988).

Histories of aquatic ecosystems outside of the Great Lakes basin include work on large rivers and estuaries in North America and Europe, before channelization for commerce (Sedell and Froggatt 1984; Dunfield 1985; Trautman 1981; Karr et al. 1985; Lelek 1989; Baumann et al. 1974; Regier et al. 1988; Schubel 1986). The general patterns and mechanisms of ecological degradation described in these histories are strongly analogous to those of the Great Lakes, and many of the lessons from these histories also apply to the Great Lakes.

Practical considerations related to collection and interpretation of historical information about ecosystems

In ecology as in geology and phylogenetics, historical inference must often supplement or replace controlled, replicated experimental studies. Several kinds of scientific inference are available to those who study history or phenomena that are not susceptible to experimentation (Gould 1986). They include the following: (1) observing and measuring processes that presently occur and extrapolating their effects over historical time intervals, under a general presupposition of "uniformitarianism"; (2) reconstructing slow or historical developmental processes by observing different stages of the process in different locations (this has been called "the ergodic hypothesis" by Chorely and Kennedy (1971) or "synchronic analysis" by Amoros et al. (1986)); and (3) studying unusual structures or distributions that make sense in only one or a few historical contexts (the "panda principle" in anatomy).

Three methods, not entirely independent of those above, may be added to Gould's list: (4) "natural" or unplanned experiments, where similar systems or portions of systems may be differently affected by a "treatment" of some sort (these may be studied directly or through historical evidence); (5) retrieving information about ecosystems or their components from old documents, maps, paintings, photographs, middens, museum specimens, fossils deposits, varves, or from inter-

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Table 2. (*concluded*).

Ecosystem feature[a]							
Chemical			Biotic			Applicability	
pH	DO	P and N	Persistents	Debris	Macrophytes	Spatial[b]	Temporal[c]
M	L	L	H	—	—	Small	Short
H	H	L	H	L	M	Large	Long
L	L	L	L	L	L	Large	Long
H	H	L	M	M	M	Small	Long
L	L	L	M	—	L	Small	Medium
—	—	—	—	L	L	Large	Long
—	M	—	M	—	—	Medium	Long
—	—	—	—	M	H	Variable	Short
—	—	—	—	L	M	Large	Short
—	—	L	M	L	L	Small	Medium
L	M	M	M	L	L	Small	Medium
M	M	M	H	L	L	Small	Medium
—	M	M	M	M	M	Small	Medium
—	—	—	—	L	M	Small	Medium

views with "old timers"; and (6) hindcasting or extrapolation backwards in time using simulation models.

Both contemporary and historical ecological inference are usually extrapolated through the use of analogy and uniformitarianism. In this way, our knowledge of local or briefly observed phenomena can be applied with caution to other ecosystems in other locations (Whillans 1996).

The understanding of contemporary interactions between human activity and ecosystems is incomplete. It is common for aquatic habitats in the Great Lakes region to be subjected to a variety of insults simultaneously: toxic contaminants, nutrient loading, temperature extremes, physical restructuring, and sedimentation, all as a result of regional urban and industrial shoreline and basin development (Kelso and Cullis 1996; Kelso et al. 1996). Although scientists have had some success in unravelling the individual cause–effect relationships involved in such suites of processes, they have been more successful at identifying useful generalizations regarding the occurrence and significance of these effects in aggregate. In some cases, the cumulative effects of stressors may be impossible to sort out. The understanding of historical processes is mostly of a similar resolution; that is, we can specify only qualitative generalizations about past ecosystem states and processes. Only rarely is it possible to extract interpretable quantitative information about specific phenomena from currently available retrospective information sources (Kelso et al. 1996; Bray 1996).

When habitat is examined retrospectively it is usually in the course of either (1) a hypothesis-generating exercise (e.g., Regier et al. 1969) or (2) a heuristic synthesis of multiple relationships (e.g., Smith 1972). Some hypothesis testing is evident in the literature, particularly involving "palaeolimnological" techniques and resurveys of historic biological surveys (Charlton 1987; Hall and Ide 1987; Wichert 1991, 1994*a*, 1994*b*). Also apparent, especially in the past decade, are applications of indices using historical data: habitat suitability index (HSI), instream flow incremental methodology (IFIM), and index of biological integrity (IBI) (Steedman 1988; Karr 1991; Bray 1993). Numerous fisheries histories portray the management and societal context of fish community and habitat alteration (Egerton 1985; Regier and Baskerville 1986; Whillans and Berkes 1986; Koonce et al. 1996; White 1996; Evans et al. 1996).

Sources of retrospective information

Three primary tools for retrospective assessment can be used in conjunction with a number of secondary tools (Whillans 1985, 1996) (Fig. 2). "Accumulators" store evidence of past environments at regular rates. Growth structures in biota and varved sediments are examples. "Residues" are remnants of past environments that inadvertently serve in retrospective assessment. They include macrofossils, archaeological material, museum references for other purposes, inorganic substances in sediment cores, landscape patterns, and long-term integrative physical properties such as deep groundwater and soil temperatures (e.g., Deming 1995). "Replicates" are intentional representations of the past, such as remote imagery, written observations, data sets, and oral narratives. Secondary tools would include dating techniques, eco-indicators, spatial gradients, hindcasting models, and surrogate experiences. No tool is perfect. Combinations of tools would most probably yield the clearest results.

What level of resolution can be expected?

The resolution of retrospective answers to ecological questions will always be limited by the accuracy, extent, and spatial and temporal coverage of the historical data (Table 2). For example, diatom remains; charcoal; pollen; and chemical, radiological, and magnetic properties of sediment cores can provide a portrait of changes through a period of time and can sometimes be used to pinpoint specific events (Dearing et al. 1987; Mac-

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Donald et al. 1991; Smol 1992; Versteeg et al. 1995). In addition, air photos can provide a very accurate areal measurement of certain physical or biological features. Conversely, a historic sketch, map, or painting can provide an estimate of size, an idea of presence or absence, but cannot be quantitative.

Retrospective information is likely to be patchy in the locations and environments that it relates to. A variety of sources, each covering a different "patch", may be required to produce a high degree of resolution. However, confounding factors, such as human bias, may reduce resolution if more than one information source or technique of analysis is used.

Detailed, spatially precise retrospective analyses that would inform site-specific and parameter-specific habitat interventions are relatively rare for Great Lakes fisheries (Baumann et al. 1974; White et al. 1975; Harris et al. 1982; Holmes and Whillans 1984; Bray 1993), but exist for other locations and for wildlife habitat (Hammer 1992). Most retrospective analyses of aquatic habitat are regional in scale and must deal with extensive habitat complexes as spatial aggregations in multiyear units of time. In fact, the primary focus for most analyses has been fish species or the fish community. This should not be surprising because data on the state of fish are normally precursers to an investigation of the habitat of those fish.

What biases are likely?

Humans exist in a cultural context. Every thought, perception, record, and interpretation is influenced by our culture and assumptions about nature. As a result, human cultural bias is inherent in any historical information, i.e., the record of the past as recorded or preserved by humans. Bias also can originate because of economic considerations. Funding and contemporary priorities determine the types of information collected and preserved in the past, and they determine the types of historical analyses that are undertaken today.

In using historical information for habitat restoration work, the biases associated with the values driving resource extraction, habitat protection and restoration, and record keeping are particularly important. These values change through time and it is important to understand the values of the time in which the historical information was produced to understand the limitations of the information. This bias is evident in literature describing changes to fish populations and fish habitat. For example, much of the historic literature deals only with fish of commercial or recreational value, and the types of records kept were largely the commercial yields for those species (Regier 1979; Goodier 1981; Whillans 1979; Kelso et al. 1996). In some cases, what is now recognized as habitat destruction was described as stream "improvements", e.g., removing obstacles from rivers to drive logs and removing coarse fish in the Nipigon River to help sustain brook trout populations (Kelso and Demers 1993; White 1996).

"Creating future history": how can ecological information that is critical to future understanding be gathered and preserved today?

Most managers and researchers working for natural resource agencies would agree that it is a difficult job to design, implement, and apply relevant research for today's problems, without worrying about tomorrow's! Out of the enormous volume of scientific, technical, and cultural information that is being collected in the Great Lakes region, how is it possible to make good guesses about the data that will be crucial for future historical analyses of Great Lakes aquatic habitats? Should this be a concern?

Natural resource or environmental agencies and universities maintain records of routine environmental monitoring networks or collect data, specimens, or publications from a variety of sources. In the past, preservation of such materials was best assured if they ended up in municipal, state, provincial, or national archiving institutions or museums. However, such materials were often discarded in routine housecleaning at some time after the material lost its contemporary relevance but before it acquired a patina of historical value or relevance. The preservation of digital data or documents may pose particularly urgent problems related to the physical durability of the medium that data are recorded on or to the transience of the technology required to read the data (Rothenberg 1995). Institutions can increase the likelihood of data survival by ensuring that important information is published on paper in some form and deposited in libraries and archives. Material left unpublished in filing cabinets rarely outlasts the original owner of the filing cabinet.

The following should be considered when evaluating the future significance of environmental documents, specimens, or data: (1) Is the material unique? (2) Is it already part of the public record in journal publications in libraries? (3) Does the material record information about a resource or habitat that is likely to be transformed through land development or other destructive process? (4) Is the material already old and of historical interest? (5) Is the material unlikely to be collected again because of high cost, logistics, or unique circumstances? (6) Will storage be costly because of the volume or special environmental requirements of the material? (7) Can the information be stored only in digital format?

A number of long-term ecological research (LTER) programs and networks exist in North America but are poorly represented in the Great Lakes basin. The explicit aim of LTER is to design research that addresses the rare, slow, or transient ecological processes in a way that facilitates historical and comparative analysis and interpretation. Data records from North American LTER sites extend back 50 yr in some cases (Franklin et al. 1990). In the future, LTER data archives will be a logical starting point for data relevant to long-term ecological phenomena. "State of the Environment" reporting has gained prominence in the Great Lakes basin. It has been used by both government (Bird and Rapport 1986) and nongovernmental groups (Colborn et al. 1990) as an environmental census. The focus is on indicators of problems and successes in the stewardship and manipulation of environmental factors, including fisheries.

Conclusion: using historical information to influence habitat management

Decisions relating to aquatic habitat restoration can probably address only two alternatives: (1) "as it used to be" (a design based explicitly on the understanding of some historical state at that location) and (2) "as we want it to be" (a design that may incorporate any mixture of history, self-interest, or practicality (Steedman 1994)). This paper is relevant mainly to

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option 1, although the importance of historical images and human design objectives will differ in different contexts. In relatively intact, undisturbed ecosystems it could be argued that natural, historical images of ecosystems should be used exclusively to guide habitat restoration. Conversely, in relatively degraded ecosystems, where natural ecosystem functions and composition are impaired or destroyed (i.e., the natural option has been lost), it is inevitable that human designs will have more influence. Even in this case, native ecosystem components, with their history of co-adaptation to regional conditions, will probably represent a "best bet" for habitat restoration (Ryder and Kerr 1990).

In relatively undisturbed landscapes, benchmarks or standards for healthy ecosystems (or ecosystem components) may exist and may be characterized directly. Otherwise, knowledge of intact ecosystems can only be based on historical information of the kind discussed here. In some cases, benchmarks can be developed from a mixture of empirical, theoretical, or cultural information and opinion.

Historical analysis establishes a conceptual context for habitat conservation and restoration in the Great Lakes, in which the quantitative details must be supplied by contemporary ecological research and theory. Assuming some consensus regarding the relevance of historical benchmarks for restoration, historical information can influence the science and management of aquatic habitat by supporting documentation of historical benchmarks for species composition, habitat features, and landscapes prior to industrial development (Steedman 1994). Historical benchmarks can range from the highly descriptive to the highly quantitative, depending on the context and information sources. Because of the evocative nature of good local descriptions of pre-industrial ecosystems, this often proves to be one of the most important catalysts for restoration of degraded ecosystems. In such cases, the momentum and priority accorded to preservation and restoration of "cultural heritage" can sometimes be transferred to the preservation and restoration of "natural heritage", particularly in urban areas where degradation has been most acute.

Historical information has significant potential to direct aquatic habitat management in the Great Lakes and has already contributed to the acceptance of historical calibrations for binational initiatives related to water quality, fisheries (particularly regarding re-establishment of lake trout and Atlantic salmon), and habitat conservation and restoration in the Great Lakes basin (e.g., Lake Superior Binational Program 1995; International Joint Commission 1988; EC and OMNR 1984; Francis et al. 1979). Although the use of historical information has been opportunistic (it is limited by the preservation of information in specific forms) and generally of low resolution (it is generally semiquantitative at best), the products of these analyses have been compelling (they have changed the attitudes and expectations of people) and surprising (many of the conclusions of historical analysis were not predictable from other sources).

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Are habitat rehabilitation initiatives uncoupled from aquatic resource management objectives in the Great Lakes?

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Abstract: Surveys of the 43 Great Lakes Areas of Concern have documented an increased recognition of the need for habitat rehabilitation and conservation. Although habitat rehabilitation and conservation initiatives are underway in all Areas of Concern, there appears frequently to be a lack of connection between habitat rehabilitation initiatives and aquatic resource management objectives and the scientific method. This could be addressed by (1) placing a higher priority on establishing quantitative fish community and habitat objectives for Areas of Concern to help evaluate and select appropriate habitat rehabilitation techniques; (2) increasing research and assessment efforts to quantify habitat-related problems, establish cause–effect relationships, evaluate and select appropriate habitat rehabilitation techniques, and quantify effectiveness relative to ecosystem structure and function; and (3) pooling available data on habitat rehabilitation effectiveness to provide the basis for application of successful tools in other parts of the Great Lakes basin ecosystem.

Résumé : D'après les relevés effectués dans les 43 secteurs préoccupants des Grands Lacs, on reconnaît de plus en plus la nécessité de restaurer et de conserver l'habitat. Si des opérations sont en cours dans ce sens dans toutes les zones critiques, il semble y avoir souvent un manque de lien entre les opérations de restauration et les objectifs de gestion des ressources aquatiques d'une part et la méthode scientifique d'autre part. On pourrait y remédier : (1) en accordant une plus forte priorité à l'établissement d'objectifs quantitatifs en matière de communauté ichtyenne et d'habitat pour les secteurs préoccupants afin d'évaluer et de choisir plus facilement les techniques de restauration de l'habitat qui conviennent ; (2) en intensifiant la recherche et l'évaluation pour quantifier les problèmes liés à l'habitat, établir des rapports de cause à effet, évaluer et choisir les techniques de restauration de l'habitat qui s'imposent, et quantifier leur efficacité sous le rapport de la structure et de la fonction des écosystèmes; (3) en regroupant les données dont on dispose sur l'efficacité de la restauration de l'habitat afin de poser les bases de l'utilisation, dans d'autres parties de l'écosystème du bassin des Grands Lacs, des outils qui ont donné de bons résultats.
[Traduit par la Rédaction]

Introduction

Although numerous laws, policies, and programs exist to enhance habitats in the Great Lakes basin ecosystem, there is a need to improve their implementation, a need for a strategic approach to habitat protection and restoration, and a need to make full use of all potential partnerships (Dodge and Kavetsky 1994). One program where there is a concerted attempt to make these required changes, is the Great Lakes Remedial Action Plan (RAP) program (Koonce et al. 1996). RAPs utilize an ecosystem approach to restore impaired uses in 43 degraded areas of the Great Lakes (i.e., Areas of Concern). This paper reviews and evaluates the status and prospects of aquatic habitat rehabilitation and conservation efforts in Great Lakes Areas of Concern from an ecosystem-based, management perspective, using recent RAP program and associated habitat surveys (Hartig 1993*a*, 1993*b*; Hartig and Law 1994; Hartig and Bradburn 1995; Kelso and Hartig 1995). We also evaluate whether habitat rehabilitation initiatives are well integrated with aquatic resource management objectives in Areas of Concern (Kelso et al. 1996).

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Background on the Remedial Action Plan program

The concept of RAPs originated from a 1985 recommendation of the International Joint Commission's (IJC's) Great Lakes Water Quality Board (IJC 1985). The Board found that, despite regulatory and resource management programs, beneficial uses (e.g., unrestricted human consumption of fish, unrestricted disposal of dredged sediments from harbors and rivers, successful reproduction of fish and wildlife species, fish and wildlife habitat) were not being restored and recommended that RAPs be developed and implemented to restore all beneficial uses in Great Lakes Areas of Concern (Fig. 1). The 1987 Protocol amending the Great Lakes Water Quality Agreement (GLWQA) formalized the RAP program and defined Areas of Concern as "geographic areas that fail to meet the general or specific objectives of the Agreement where such failure has caused or is likely to cause impairment of beneficial use or of the area's ability to support aquatic life" (IJC 1987).

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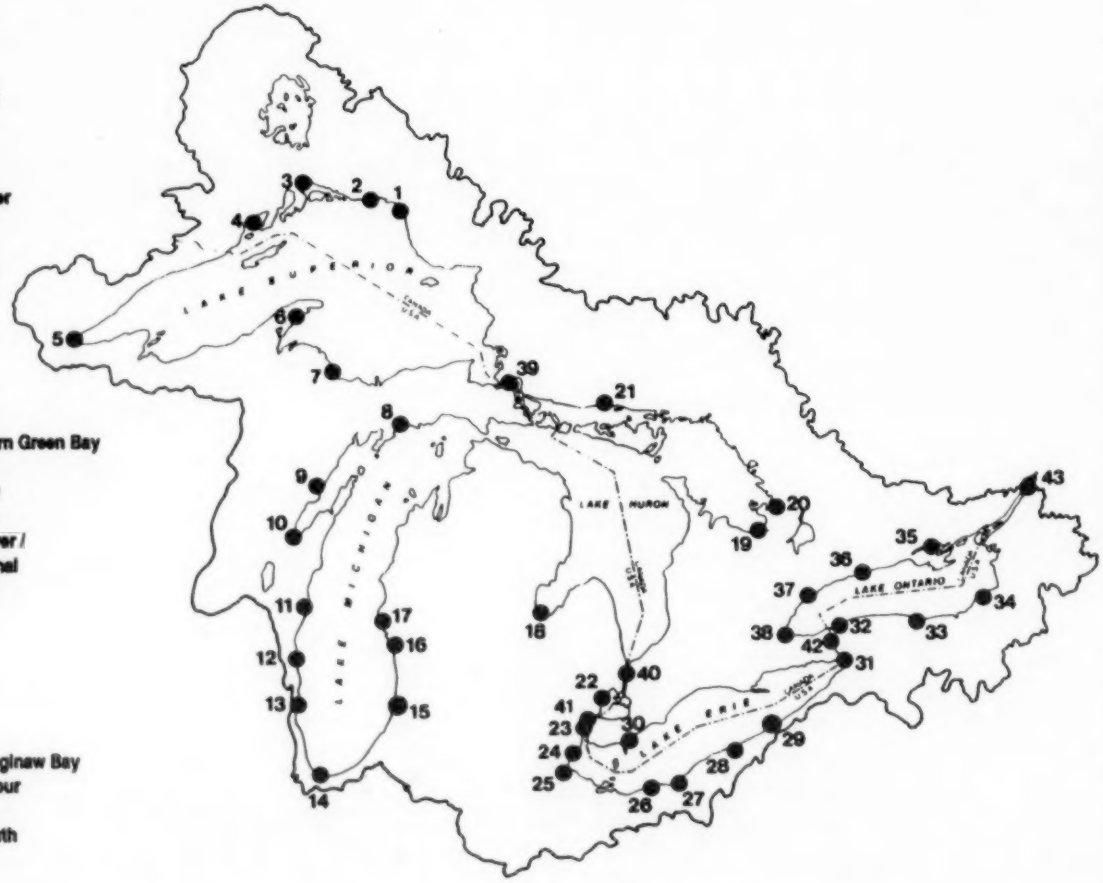
Fig. 1. Fory-three Areas of Concern in the Great Lakes basin.



Lake Superior

1 Peninsula Harbour
2 Jackfish Bay
3 Nipigon Bay
4 Thunder Bay
5 St. Louis Bay / River
6 Torch Lake
7 Deer Lake - Carp Creek / River

Lake Michigan

8 Manistique River
9 Menominee River
10 Fox River / Southern Green Bay
11 Sheboygan River
12 Milwaukee Estuary
13 Waukegan Harbor
14 Grand Calumet River / Indiana Harbor Canal
15 Kalamazoo River
16 Muskegon Lake
17 White Lake

Lake Huron

18 Saginaw River / Saginaw Bay
19 Collingwood Harbour
20 Severn Sound
21 Spanish River Mouth

Lake Erie

22 Clinton River
23 Rouge River
24 River Raisin
25 Maumee River
26 Black River
27 Cuyahoga River
28 Ashtabula River
29 Presque Isle Bay
30 Wheatley Harbour

Lake Ontario

31 Buffalo River
32 Eighteen Mile Creek
33 Rochester Embayment
34 Oswego River
35 Bay of Quinte
36 Port Hope
37 Metro Toronto
38 Hamilton Harbour

Connecting Channels

39 St. Marys River
40 St. Clair River
41 Detroit River
42 Niagara River
43 St. Lawrence River (Cornwall / Massena)

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Table 1. Status of degradation of fish populations and loss of fish habitat in Great Lakes Areas of Concern (1989, 1991, 1994).

Year	Total no. of Areas of Concern	No. of Areas of Concern which acknowledged degradation of fish populations	No. of Areas of Concern which acknowledged loss of fish habitat
1989[a]	42	16 (38%)	17 (40%)
1991[b]	43	24 (56%)	24 (56%)
1994[c]	43	29 (67%)	34 (79%)

[a]IJC (1989).
[b]IJC (1991).
[c]Hartig and Law (1994).

Impairment of beneficial use means a change in the chemical, physical, or biological integrity of the Great Lakes System sufficient to cause any of the following: (1) restrictions on fish or wildlife consumption; (2) tainting of fish and wildlife flavor; (3) degradation of fish and wildlife populations; (4) fish tumors or other deformities; (5) bird or animal deformities or reproductive problems; (6) degradation of benthos; (7) restrictions on dredging activities; (8) eutrophication or undesirable algae; (9) restrictions on drinking water consumption, or taste and odor problems; (10) beach closings; (11) degradation of aesthetics; (12) added costs to agriculture or industry; (13) degradation of phytoplankton and zooplankton populations; or (14) loss of fish and wildlife habitat.

The 1987 Protocol to the GLWQA also called for RAPs to embody a comprehensive and systematic ecosystem approach and to ensure public consultation throughout the process (Hartig and Vallentyne 1989). Each RAP is to be submitted to the IJC for review at three stages: (1) problem definition, (2) evaluation and selection of remedial and preventive actions, and (3) confirmation of use restoration. The RAP Program is described further by Hartig and Law (1994), and Hartig and Zarull (1992).

Sources of habitat data for Areas of Concern

Hartig (1993*a*, 1993*b*) surveyed managers responsible for fishery management planning in Areas of Concern to document fish community and habitat goals, objectives, or targets relative to GLWQA use impairments and current resource status of the fishery. Hartig and Law (1994) described the status of the 14 use impairments in all Areas of Concern. Hartig and Bradburn (1995) summarized the nature and extent of aquatic habitat rehabilitation and conservation initiatives in Areas of Concern. Kelso and Hartig (1995) compiled methods of modifying habitat to benefit the Great Lakes basin ecosystem.

Status of management efforts

Between 1989 and 1994, there was a 50% increase in the number of RAP teams for Areas of Concern that acknowledged loss of habitat as a serious problem (Table 1). Similar trends in increasing recognition of loss of habitat and the need for habitat rehabilitation and conservation are evident in lakewide management plans (LAMPs) for the Great Lakes and by the lake committees established under the auspices of the Great Lakes Fishery Commission to develop fish community objectives called for in the Joint Strategic Plan for Management of Great Lakes Fisheries (Koonce 1994).

Degraded fish populations are recognized in 29 of the 43 Areas of Concern and loss of fish habitat is recognized in 34 of the 43 Areas of Concern (Table 2). Although degraded fish and wildlife populations and loss of habitat are recognized, quantitative targets for restoration are often lacking, particularly for habitat (Table 2). Consequently, priority should be placed on establishing quantitative fish community and habitat objectives, targets, or end points for Areas of Concern to direct remedial efforts, to aid in selection of appropriate habitat rehabilitation techniques, and to measure progress.

Priority must also be placed on ensuring that quantitative targets and end points for Areas of Concern are complementing and supporting lakewide objectives, targets, and endpoints (i.e., those being developed under LAMPs and the Joint Strategic Plan for Management of Great Lakes Fisheries). Indeed, experience has shown that agreement on quantitative objectives and targets is essential for providing strategic management direction and clarity, and for demonstrating success (Hartig 1993*a*). Unfortunately, current goals and objectives (Kelso et al. 1996) established by RAPs are frequently at odds with those developed in lakewide management initiatives. For example, in Lake Ontario yellow perch (*Perca flavescens*) are seen as requiring lakewide restoration (an historic decline presumed), but, locally, maintenance of current abundance is the objective. Further, local and lakewide differences exist relative to the focus upon desired species (i.e., local concern may be for warmwater species while the lakewide focus is upon coldwater species). The consequence of conflicting goals and undefined targets is likely to be undirected management.

Habitat rehabilitation and conservation projects are underway in the watersheds of all 43 Areas of Concern (Table 3; Hartig and Bradburn 1995). Wetland rehabilitation or preservation (29 Areas of Concern) and shoreline and streambank stabilization (27 Areas of Concern) were most frequent. Rehabilitating and preserving wetlands has received a high priority because of severe historical losses throughout the basin (Dodge and Kavetsky 1994) and the relatively recent public acknowledgement of wetland values and functions (providing breeding, nesting, feeding, and nursery grounds for fish and wildlife, stabilizing and maintaining water tables, minimizing erosion, providing natural filtration of pollutants, providing groundwater recharge, providing recreational opportunities). There is also a high priority for shoreline and streambank stabilization (Environment Canada and Ontario Ministry of Environment and Energy 1994; Roseboom 1994) in Areas of

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Table 2. Status of fish and wildlife population and habitat use impairments, and establishment of quantitative objectives–targets in Great Lakes Areas of Concern.

Area of Concern	Degredation of fish and wildlife populations*		Loss of fish and wildlife habitat*	
	Impaired use	Quantitative objectives – targets established	Impaired use	Quantitative objectives – targets established
Peninsula Harbour	X	X	X	
Jackfish Bay	X	X	X	
Nipigon Bay	X	X	X	
Thunder Bay	X	X	X	
St. Louis River	X		X	
Torch Lake				
Deer Lake – Carp River and Creek				
Manistique River			X	
Menominee River	X	X	X	
Fox River – Green Bay	X	X	X	
Sheboygan River	X		X	
Milwaukee Estuary	X		X	
Waukegan Harbor	U		X	
Grand Calumet River – Indiana Harbor Canal	X		X	
Kalamazoo River			X	
Muskegon Lake	X	X	X	
White Lake	X		X	
Saginaw River - Bay	X	X	X	
Collingwood Harbour	R	X	R	
Severn Sound	X	X	X	
Spanish Harbour	X		U	
Clinton River	X		X	
Rouge River	X		X	
River Raisin				
Maumee River	X	X		X
Black River	X	X	X	X
Cuyahoga River	X	X	X	X
Ashtabula River	X	X	X	X
Presque Isle Bay				
Wheatley Harbour			X	
Buffalo River	L		X	
Eighteenmile Creek				
Rochester Embayment	X		X	
Oswego River	X		X	
Bay of Quinte	X		X	
Port Hope Harbour				
Metropolitan Toronto	X	X	X	
Hamilton Harbour	X	X	X	X
St. Marys River	X		X	
St. Clair River			X	
Detroit River			X	
Niagara River (Ontario)	X	X	X	
Niagara River (New York)	L		X	
St. Lawrence River (Cornwall, Ont.)	X		X	
St. Lawrence River (Massena, N.Y.)	L		X	

*X, present; U, under assessment; R, restored; L, likely.

Concern because government programs provide resources to reduce nonpoint source pollutant inputs and simultaneously enhance habitat.

Other common rehabilitation projects included channel modification (10 Areas of Concern), rehabilitation of trout spawning habitat (10 Areas of Concern), creation of bird or waterfowl habitat (12 Areas of Concern), re-establishment of native species (12 Areas of Concern), and barrier construction to exclude unwanted biota (10 Areas of Concern). These projects were seen as priorities to maximize diverse, native speciation, minimize exotic or unwanted species, and compensate for historical losses of habitat (partly as a result of channelization).

Kelso and Hartig (1995), in their compilation of habitat

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Table 3. Aquatic habitat rehabilitation and conservation projects implemented in Area of Concern watersheds, 1994.

AREA OF CONCERN WATERSHED	Habitat Components Incorporated Into Marina-Breakwall-Dock Design	Channel Modification	Floodplain Rehabilitation and Instream Cover Enhancement	Wetland Rehabilitation or Preservation	Shoreline or Streambank Stabilization	Island Construction	Excavation of Shallow Embayments to Enhance Habitat	Construction of Fishway With Habitat Enhancements	Concurrent Sediment Remediation and Habitat Rehabilitation	Creation of Bird - Waterfowl Habitat	Purchase of Land for Preservation of Pristine Habitat	Construction of "Lunker" or Other Wooden Structures	Reestablishment of Native Flora and Fauna	Preservation of Biodiversity	Use of Rights of Way to Reconnect Biological Corridors	Construction of Barriers to Exclude Unwanted Biota	Flow Modification or Alteration	Construction of Artificial Reef	Rehabilitation of Bass Spawning Habitat	Rehabilitation of Walleye Spawning Habitat	Rehabilitation of Trout Spawning Habitat	Rehabilitation of Northern Pike Spawning Habitat	Rehabilitation of Perch Spawning Habitat	Rehabilitation of Sunfish Spawning Habitat	Rehabilitation of Crappie Spawning Habitat	Rehabilitation of Shiner Spawning Habitat	Rehabilitation of Lake Sturgeon Habitat	Rehabilitation of Salmon Spawning Habitat	Rehabilitation of Reptile and Amphibian Habitat
Peninsula Harbour	X												X																
Jackfish Bay													X								X								
Nipigon Bay	X	X	X	X									X								X								
Thunder Bay	X		X		X	X	X	X	X				X			X			X	X		X	X						
St. Louis River				X	X					X	X		X			X													
Torch Lake					X																								
Deer Lake - Carp River				X	X																								
Menominee River				X																									
Fox River - Green Bay				X												X				X									
Sheboygan River				X	X							X				X					X							X	
Milwaukee Estuary				X	X				X				X																
Waukegan River		X		X	X							X																	
Grand Calumet River - Indiana Harbor Canal														X	X														
Kalamazoo River		X			X											X					X								
Muskegon Lake				X	X																X								
White Lake				X	X							X									X							X	
Saginaw River - Bay				X	X											X													
Collingwood Harbour				X						X									X		X	X	X						X
Severn Sound				X	X											X													
Spanish Harbour				X	X																								
Clinton River					X							X					X				X								
Rouge River		X	X	X	X					X		X		X			X				X								
River Raisin					X						X																		
Maumee River				X	X					X						X													
Black River				X	X													X											
Cuyahoga River					X													X											
Ashtabula Creek				X					X																				
Presque Isle Bay										X		X												X					
Wheatley Harbour				X																									
Buffalo River					X				X	X																			
Eighteenmile Creek				X																									
Rochester Embayment				X																		X							
Oswego River		X			X							X					X				X								
Bay of Quinte		X		X						X			X			X													
Port Hope																													
Metro Toronto				X	X	X		X		X			X					X				X							X
Hamilton Harbour		X		X		X		X		X			X			X			X			X	X	X	X	X			X
St. Marys River		X		X	X								X														X		
St. Clair River				X	X					X			X	X															X
Detroit River		X		X	X	X			X	X	X																		
Niagara River (Ontario)				X																									
Niagara River (New York)				X	X				X	X			X									X							
St. Lawrence River (Ontario)		X			X																								
St. Lawrence River (New York)																											X		

rehabilitation methods which benefit ecosystems, found that 6% of the projects reported in the Great Lakes were related to conservation, 34% involved wetland creation or preservation, 25% focussed on riparian habitats, and 42% related to creating reproductive habitat for fish and birds. Whether these methods reflect local concerns or are motivated by opportunities for resources (funding, local expertise) is uncertain.

Assessing the value of habitat modification

Many of the rehabilitation projects did not have strong monitoring and assessment components. However, in 10 Areas of Concern preliminary investigations were underway to help evaluate rehabilitation options and to help design statistically valid assessment procedures. Unfortunately, in 16 Areas of

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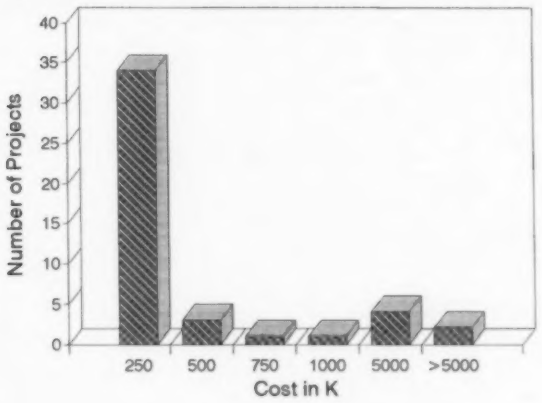
Fig. 2. Cost–frequency histogram for 47 habitat rehabilitation projects compiled by Kelso and Hartig (1995).



Concern either no assessment or monitoring was underway or planned, or teams simply relied on routine electrofishing surveys every 3–5 yr to track general status and trends. This routine monitoring appeared to lack spatial and temporal resolution adequate to document effects on ecosystem structure or function.

As of 1994, only 16 Areas of Concern had habitat rehabilitation projects with monitoring and assessment components designed to document effects on ecosystem structure or function. The 16 Areas of Concern included: Nipigon Bay (5-yr restoration plan), Thunder Bay (5-yr restoration plan), Fox River – Green Bay (three walleye habitat projects), Collingwood Harbour (Black Ash Creek Restoration Project), Severn Sound (5-yr rehabilitation program), Rouge River (Johnson Creek Project), Maumee River (Metzger Marsh), Black River (Lorain Reef Project), Cuyahoga River (Lakewood Reef), Rochester Embayment (Conesus Lake Project), Oswego River (Finger Lake Trout Habitat Project), Metropollitan Toronto (wetland restoration projects, artificial reef construction, shoreline naturalization), Hamilton Harbour (5-yr rehabilitation project), St. Clair River (Stag Island and Chenal Ecarte – Syndenham River Habitat Projects), Detroit River (Ruwe Marsh Project; Detroit Metropolitan Airport Wetland Mitigation Project), and Niagara River (Strawberry Island Project). It should be noted that there were other projects in these 16 Areas of Concern with monitoring that was insufficient to document effects on ecosystem structure and function.

Assessing the benefits of habitat rehabilitation to ecosystems may be rather subjective. Where assessment was part of an initiative to rehabilitate habitat in the Great Lakes (Kelso and Hartig 1995), 62% assessed only whether the habitat was altered (presumably with no associated detrimental effects). For those that attempted to quantify change or benefit to ecosystem performance, 38% were unable to assess either whether the expected change occurred or the relative amount of change.

Coupling habitat initiatives with ecosystem objectives

A comparison of the number and diversity of habitat rehabilitation projects underway in Area of Concern watersheds (Table 3) with quantitative fishery and habitat objectives and targets (Table 2) indicates that habitat rehabilitation and conservation are often not directly related to quantitative ecosystem objectives or targets. Habitat rehabilitation projects appear to frequently be opportunistic. Projects seem to result from initiative or interest of a local fishing club, nonpoint source and erosion control programs that can enhance habitat, local interest to preserve or restore wetlands, opportunities through mitigation settlements, or other initiatives. In 1993 and 1994, there appeared to be little connection between habitat rehabilitation projects and aquatic resource management objectives in Areas of Concern. If the intent of management is to achieve a desired future state of ecosystems through use of quantitative objectives and targets, then higher priority should be placed on establishing quantitative objectives to evaluate and select appropriate habitat tools and implement priority actions.

A simple conceptual model for habitat (i.e., the relationship between physical habitat and ecosystem structure and function) is also needed. This system model would: (1) describe habitat components in an understandable fashion; (2) ensure that habitat inventories and data are in a form that can be accessed and used by management; (3) recognize and account for time, space, and natural and human-induced variability; (4) recognize that habitat rehabilitation and conservation will often be implemented in an adaptive management context (based on experiments and demonstration projects); and (5) ensure that adequate data and information on impacts of habitat alterations on ecosystem structure and function are available.

This simple conceptual model for thinking about habitat could be used in multistakeholder processes to rehabilitate and preserve the Great Lakes. Individuals and organizations involved in habitat must establish closer working relationships with organizations responsible for water quality, land-use planning, recreation, and other interests. The intent should be to develop a community of common interests and to build the capacity to rehabilitate and preserve the entire Great Lakes basin ecosystem.

Setting priorities

If one agrees that habitat rehabilitation projects should be implemented in an adaptive management context, priorities must be set to expend resources on a cost- and ecosystem-effective basis. In general, adaptive management calls for setting priorities, implementing actions, and measuring effectiveness in an iterative fashion for continuous improvement (Holling 1978). The Nature Conservancy (1994) uses a biodiversity framework to identify unique elements of Great Lakes' biodiversity, human activities which place biodiversity at risk, and priority actions to preserve unique elements of biodiversity. The Nature Conservancy (1994) recommends four actions to protect biodiversity: (1) developing strategically coordinated, local projects that address collectively the most significant systems and stresses; (2) improving the basic and applied science necessary for biodiversity conservation; (3) increasing awareness of the basin's biodiversity and of methods to conserve that biodiversity; and (4) increasing the support of regional institu-

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tions, governmental and private, for the protection of biodiversity.

The Pacific Rivers Council (1993) also developed a strategy to set ecosystem priorities. Ecologically healthy watersheds require the maintenance and protection of the lateral, longitudinal, and vertical connectedness of the mosaic of habitat patches and ecosystem components within the watershed over time. However, most watersheds are already degraded and fragmented. Relatively healthy undisturbed headwaters, riparian areas, biotic refugia (i.e., areas with relatively undisturbed, healthy habitat and processes that serve as refuges for biodiversity), and biological "hot spots" play a vital role in supporting existing health for the system and in anchoring recovery efforts. As an initial step, the Pacific Rivers Council (1993) recommends identifying and protecting relatively healthy headwaters, biotic refugia, riparian areas, floodplains, and smaller intact riverine habitats throughout the watershed. Following protection of these healthy areas, begin to rehabilitate the reaches between protected healthy areas and eventually link the healthy areas. This approach calls for active participation of local communities and citizens in implementing the steps and actions. The approach contrasts with traditional rehabilitation strategies that target the majority of resources on rehabilitating the most degraded reaches with little regard for the need of the overall ecosystem or for the opportunities for cost-effective, rapid biotic recovery (Pacific Rivers Council 1993).

These are two examples of priority setting frameworks. We encourage evaluating and developing others.

Concluding remarks

Environment Canada and the U.S. Environmental Protection Agency identified the need for greater will to conserve and rehabilitate habitats (Dodge and Kavetsky 1994). This call for greater will to conserve and rehabilitate Great Lakes habitats reflects a sincere sentiment to see the right things get done quickly, but Zarull (1994) recognizes the uncertainty in our knowledge of how systems do and should function and the paucity of information that defines problems. Actions to rehabilitate and restore degraded environments should be based on an understanding of causes and predicted results. Adequate assessment, research, and monitoring are essential to define problems, establish cause–effect relationships, evaluate remedial options, select remedial actions, and document effectiveness. Such assessment, research, and monitoring are the foundation of ecosystem-based management, and, in the end, have proven to save money for both the public and private sectors (Zarull 1994). The cost alone of habitat rehabilitation and conservation underscores the need for effective ecosystem assessment and monitoring. In the Great Lakes, implementation costs exceed $0.5 million in 14% of 47 habitat initiatives compiled by Kelso and Hartig (1995) (Fig. 2). Only 27% of these initiatives cost less than $20 000.

An uncoupling of habitat rehabilitation initiatives from aquatic resource management objectives and the scientific method in Areas of Concern could be addressed by: (1) placing a higher priority on establishing quantitative, fish community and habitat objectives, targets, or endpoints for Areas of Concern and other affected areas to help evaluate and select appropriate habitat rehabilitation techniques; (2) increasing research and pre- and post-project assessment efforts to quantify habitat-related problems, establish cause–effect relationships, evaluate and select appropriate habitat rehabilitation techniques, and quantify effectiveness relative to ecosystem structure and function; and (3) pooling available data on habitat rehabilitation effectiveness to provide the basis for application of successful tools in other parts of the Great Lakes basin ecosystem.

These recommendations strengthen the scientific basis for habitat management actions and help fulfil the commitment for use of a systematic and comprehensive ecosystem approach in management of the Great Lakes (IJC 1987; Great Lakes Fishery Commission 1992).

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Ensuring sustainability of natural resources: focus on institutional arrangements

Marjorie M. Holland

Abstract: Sustainable management of regions and watersheds presents a quandary. Because of the large scale of regions and of the environmental problems associated with them, sustainable management is best directed by an entity with a large purview. However, experience suggests that effective and efficient solutions to environmental problems are best developed by involving natural and social scientists possessing knowledge of fundamental principles in their respective disciplines with local stakeholders who understand both the local resources and the users of those resources. The last decade has seen a shift toward consideration of the "human dimensions" of natural resource management. Nearly 20 years ago, a mechanism was created in Massachusetts to provide advice on sustainability of water resources: the reasons for the success of that mechanism are worth examining today. Through the creation of a Citizens Advisory Committee, there was agreement among scientists, managers, planners, and policymakers to adopt a landscape perspective, using natural rather than political boundaries in setting management goals as well as for development of the institutional arrangements necessary for management of ecological systems.

Résumé : La gestion durable de régions ou de bassins versants pose un dilemme. La grande étendue des régions et des problèmes environnementaux qui leurs sont associés fait que leur gestion durable est le mieux orientée par une entité de grande envergure. L'expérience porte cependant à croire que les solutions efficaces et efficientes aux problèmes environnementaux sont souvent le mieux élaborées par la coopération de scientifiques des sciences naturelles et sociales maîtrisant les principes fondamentaux de leur domaine et des intervenants locaux qui connaissent bien les ressources locales et leurs utilisateurs. Au cours de la dernière décennie, la gestion des ressources naturelles a fait une plus grande place à la «dimension humaine». Il y a près de vingt ans, un mécanisme était créé au Massachusetts dans le but de formuler des conseils sur le caractère durable des ressources en eau et les raisons de sa réussite justifient que l'on s'y intéresse. Dans le cadre d'un comité consultatif des citoyens, les scientifiques, les gestionnaires, les planificateurs et les décideurs ont convenu d'adopter un cadre «naturel» reposant sur l'utilisation des limites naturelles, plutôt que des limites politiques, pour la définition des objectifs de gestion et l'élaboration des ententes entre organismes nécessaires à la gestion des systèmes éologiques.
[Traduit par la Rédaction]

Definition

"Sustainable environmental management" is the management of human activities and their impacts over time such that they neither irreversibly degrade the environment, nor impede the systems' ecological structures or functions (Barnthouse et al., in press).

Sustainable management goals

The management of human activities that often cross jurisdictional boundaries (and their impacts within landscapes and watersheds), is best served through the use of natural rather than political boundaries in setting management goals. Management strategies should utilize watershed boundaries or airsheds to consider such regional processes as acid deposition. The need to look at natural resource problems from a perspective larger than that used traditionally applies to managers, planners, and policy makers. There is a need for a landscape perspective in scientific research as well as in management of ecological systems (Holland 1993).

To insure the success of any sustainability-based environmental management program, a major public outreach campaign on the meaning and importance of the concept of sustainability will be essential. Positive rewards for individuals, or for society, acting and managing for the long term would help usher in sustainability. At present, there seems to be a lack of economic or legal incentives to encourage sustainable behavior.

Another goal of a sustainability-based environmental management program is to manage human activities and their impacts within a longer time frame, i.e., generations rather than 1 or 2 years at a time. We presently have 1-year budgetary cycles in government and academia. Similarly, corporations tend to be driven by short-term profits, which may ultimately prove to be contrary to their long-term interests. Society must think and plan in longer time steps to achieve sustainable environmental management. Appropriate planning time frames will depend on the issue, but in general, a 5- to 10-year planning cycle, coupled with a visionary, long-range 50- to 100-year planning process would help assure that proposed human activities and impacts are, in fact, sustainable. This planning approach with an appropriate time frame would allow us to sustain ourselves, while providing resources for fu-

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Table 1. Essential ecosystem properties.

1.	Adequate water, soil (sediment), and air quality (including Hydroperiods)
2.	Diversity and adequate quantity of habitat types
3.	Viable populations of diverse native species (gene pool)
4.	Resilience (structural and functional) and regenerative ability
5.	Self-sustaining (minimum subsidy; minimal ecological management)
6.	Connectivity

ture generations. We would do well to require that proposed activities pass a prospective longevity test. That is, those who propose new activities should demonstrate that their activity could be sustained without unacceptable ecological damage (Barnthouse et al., in press).

The challenge within sustainability-based landscape management is to find ways to address basic human needs for agricultural production or water distribution without causing unnecessary environmental problems (such as non-point-source pollution or habitat loss). At the same time, human activities must be managed to preserve essential ecosystem properties (Table 1).

"Resilience" and "connectivity" are important concepts for sustaining the life-support capabilities of landscapes and watersheds (Table 1). Resilience is the ability of a system to respond to stress. If a system is able to return in a timely fashion to its original characteristics after some form of disturbance, then it is resilient. Connectivity refers to the functional relationships in natural systems, such as the close association of a stream with its floodplain. A loss of connectivity may occur directly, through diking and channelization, or indirectly, through the regulation of flood regimes by use of navigation dams (Doppelt et al. 1993). In the case of terrestrial systems, corridors are essential to allow biota to continue to maintain viable populations in fragmented habitats (e.g., colonization, genetic exchange).

Scientific uncertainties

Sustainability in environmental management requires that effects of management actions be anticipated. However, ecologists have not come far in developing an anticipatory science. There are always scientific uncertainties related to anticipating what will happen in the environment, given the complexity and our limited understanding of interactions in the environment (Barnthouse et al., in press). Recently, however, as ecologists have been called upon to solve more environmental problems, the lack of an anticipatory capability has become more apparent. Ecologists have recently set research priorities (Lubchenco et al. 1991), the answers to which will assist in developing the anticipatory tools and designing the experiments necessary to give the discipline a more anticipatory capability.

Ecological risk assessment has uncertainties associated with it. Risk assessment is a new field that attempts to make quantitative predictions, accompanied by clear presentations of the assumptions and uncertainties involved (Suter 1993). Despite the uncertainties, the estimates generated in risk assessment have to be used in setting standards and determining needs for remediation.

Currently, it is difficult to undertake impact assessment and predict the resilience of specific systems. In some cases, recovery times can be predicted (Niemi et al. 1990). In some cases, the resilience can be predicted more accurately than the resistance, i.e., the amount of anthropogenic stress a system can withstand.

Also, it is difficult to assess how much connectivity can be disrupted before a system will collapse. Landscape patterns affect biodiversity, but the relationships are uncertain. For example, in the U.S. Pacific Northwest, the precise relationship between forest fragmentation and numbers of spotted owls still is not clear.

Human activities to protect the environment also may have unpredicted consequences. For example, as New York Harbor has become cleaner, marine wood borers have returned and are destroying pilings (Weis and Weis 1992). The human response to this unexpected event was to use more chemical control or wood preservatives that leached toxic chemicals into the system (Weis and Weis 1992), producing another problem that demanded an environmentally sensitive solution.

Scientists in the policy arena often are reluctant to state conclusions without a high statistical confidence level (95% is the standard in scientific practice). However, in light of the urgent need for informed judgements in conservation and environmental policy, scientists should become comfortable with recommending actions on the basis of weight-of-evidence, now becoming the standard in governmental practice. The International Joint Commission in its *Sixth Biennial Report on Great Lakes Water Quality* recommended a weight-of-evidence approach in matters concerning management of the Great Lakes Ecosystem (International Joint Commission ISBN 1–895085–36–5).

Sociopolitical uncertainties

Long-term thinking, scientific information, and sociopolitical receptiveness (social acceptability and political feasibility) are fundamental prerequisites to sustainable ecosystem management. While environmental management time frames and scientific uncertainties are discussed above, sources of sociopolitical uncertainty that may slow the onset of sustainability-based ecosystem management exist.

It is important to note that at all levels of management for sustainable ecosystems, public support is essential to the success of ecosystem management efforts. A major source of uncertainty is the extent to which public support can be rallied around preventative rather than curative tasks. Public education and outreach are, therefore, of paramount concern in successful landscape and watershed management efforts. To be successful, there is need for development of a joint Ecosystem Management Strategy Agreement (EMSA). Several programs exhibiting aspects of an EMSA, developed by biologists in an effort to acquire knowledge useful for management purposes (Table 2) will be described on the following pages.

Ecosystem management strategies and agreements among states and counties are subject to influence by sociopolitical factors. When political offices change hands, agreements at the ecosystem–interjurisdictional level can be reversed or rendered inactive through neglect. More formal or higher level

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Table 2. Salient features of science-based programs.

Program		Scale	Characteristics
WSCAC	Water Supply Citizens Advisory Committee	Local - regional	Effective communication with local stakeholders
MAB	Man and the Biosphere Program	National - international	Success where local stakeholders included
RAMSAR	Wetlands of International Importance	National - international	Success where local stakeholders included
SBI	Sustainable Biosphere Initiative	Regional - international	Science; consensus; news media; developing
PRC	Pacific Rivers Council	State - national	Science; principles; Congress; developing
SBP	Sustainable Biosphere Project	National - international	Science; regional approach; developing
EMAP	Environmental Monitoring and Assessment Program	Regional - national	Science; regional approach; developing

Table 3. Characteristics that led to success of Water Supply Citizens Advisory Committee (WSCAC).

1.	Vision for the future
2.	Courage to propose a new way of doing business
3.	Trust and respect among all representatives on Citizens Advisory Committee
4.	Inclusiveness of committee membership (representation of legal, economic, ecological, social, and aesthetic interests)
5.	Commitment to make process articulated in the Memorandum of Understanding work
6.	Good rapport between committee members with nonmembers and their issues
7.	Effective communication informs network members of progress
8.	Continuity of central staff from inception of the committee to present
9.	Consistent funding for office space, expenses, and staff
10.	Full-time staff answerable only to the citizens committee

agreements will be transferred more readily from one administration to the next. An agreement's active life-span will depend upon the extent to which it is flexible enough to incorporate changes in political priorities and the level of public support. For example, the Water Supply Citizens Advisory Committee, created in 1977 by an agreement between a state agency and a local organization, is created at a high level, remains flexible at the local level, has strong public support, and is active and visible (Holland 1993). In response to regional water supply concerns in the Commonwealth of Massachusetts, a Citizens Advisory Committee (CAC) was established through a Memorandum of Understanding between a state agency (the Massachusetts Metropolitan District Commission) and a local consortium of elected officials (the Massachusetts Steering Committee on the Connecticut River). This CAC (called the Water Supply Citizens Advisory Committee, or WSCAC) is a good example of the fulfillment of an EMSA, where representatives of 35 stakeholders (representing industry, local government, nongovernmental organizations, state government (from both Connecticut and Massachusetts), watershed associations, and the academic scientific community) were appointed to serve on the CAC by the Massachusetts Secretary of Environmental Affairs (Holland 1993). Expertise of the citizens serving on WSCAC has always been multidisciplinary, and has included ecologists, farmers, land use planners, industrial water engineers, environmental lawyers, municipal water managers, state agency scientists, and chief elected officials. The Memorandum of Understanding was signed in 1978, and the CAC continues to function effectively today.

The WSCAC represents an unusual approach to engaging citizen participation in water resource policy decisions. The Massachusetts Water Resources Authority (MWRA) supports the WSCAC with funding for office space, expenses, and staff. Since the inception of the Committee, it has advised the MWRA and the Metropolitan District Commission on water conservation and watershed protection strategies. The WSCAC's members regard the following as the most important lessons learned from the committee's 18 years of existence (Dawson 1988): active citizen participation is a good investment, ensuring publicly supportable, cost-effective, and environmentally sound solutions; informed citizen input on major policy decisions requires an independent, full-time staff answerable only to the citizens committee; and to gain credibility, citizen input must be sought from diverse sources. The success of the WSCAC provides a concrete example of the value an EMSA can play in sustainable environmental management.

What sets WSCAC apart from other public participation efforts has been its paid staff and inner circle of long-term volunteers. As officially designated "watchdog," and funded by the agency it watches, WSCSC has been an extraordinary exercise in citizen participation. While many volunteer committee members have contributed much time and expertise to WSCSC, the role of the central office staff has been critical in providing continuity, coordination of effort, and a single point of contact with state officials and water planners. Essentially the same staff members have served as the nucleus of WSCAC from its inception to the present (Platt 1995).

The WSCAC experience demonstrates the importance of the makeup of the groups charged with developing proposed agreements (Table 3). Group membership that is technically oriented can produce a scientifically sound approach that lacks political viability. Groups weighted toward policy-makers can ignore essential scientific realities such that the plans do not produce the intended benefits to the resource. It is important for groups designing sustainable ecosystem management strategies to have, within their ranks, experts in both policy and science. Most important, these groups should have at the table individuals who are leaders in the region, including individuals who are active with and trusted by the region's political and economic power bases.

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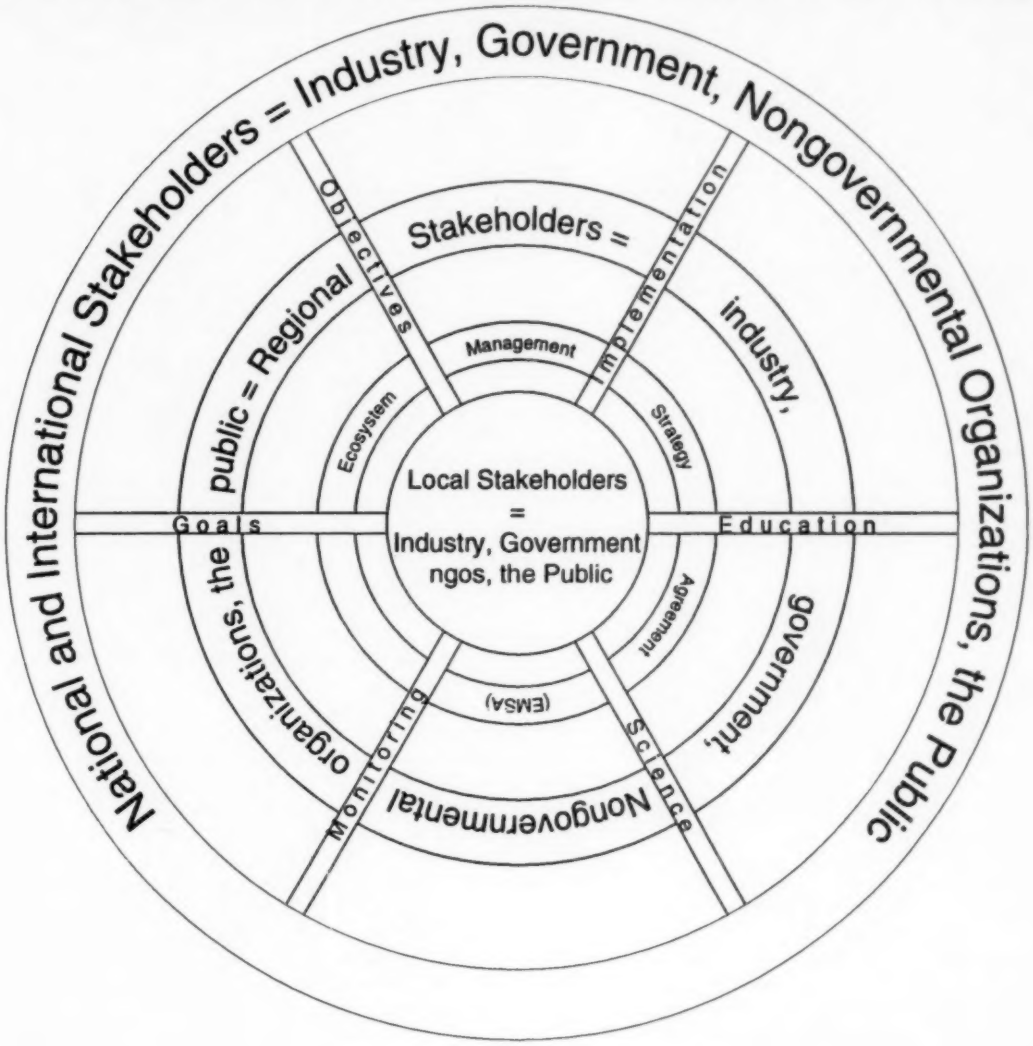
Fig. 1. A general strategy for sustainable management of regional ecosystems where the EMSA operates close to the local stakeholders.



A strategy for sustainable management of regions

Sustainable management of human activities and impacts in terms of regions and watersheds presents a quandary. Because of the large scale of regions (denotes both regions and watersheds) and the environmental problems associated with them, environmental management decisions must be directed by an entity with a large purview. However, experience suggests that effective and efficient solutions to environmental problems are best developed by involving local stakeholders who understand the resources and users of the resources. Therefore, a general model of the types of interactions needed to support sustainable management of regional resources (an EMSA) that attempts to reconcile these observations is outlined (Fig. 1), using WSCAC as an example.

Such broad environmental goals as attainment of fishable and swimmable waters and preservation of species are set by national governments. Ecosystem-specific goals, best accomplished at the regional or watershed scale, are delegated, however, to regions. Governmental bodies (states, counties, or cities) within the region are responsible for jointly refining and accomplishing ecosystem–interjurisdictional goals.

An EMSA is a strategy agreed upon by relevant governments within a region to manage human activities in a given regional ecosystem to accomplish particular goals (Barnthouse et al., in press). This strategy would involve authorizing and chartering a regionally based interjurisdictional entity to define and analyze problems and develop specific objectives that would accomplish regional goals. An advisory committee for such an entity includes jurisdictions, representatives or stakeholders, the general public, and technical experts, as in the case

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of the WSCAC in the Commonwealth of Massachusetts (Table 3).

Success for an EMSA depends on a high level of communication among all stakeholders involved. Thus, a diagram of a general strategy for sustainable management of regional ecosystems (Fig. 1) shows six spokes of a wheel, with each spoke indicating the type of information to be communicated among local, regional, national, and international stakeholders. The cross-cutting topics to be communicated include goals, objectives, implementation strategy, educational information, scientific knowledge, and results of monitoring or investigation. For an EMSA to be effective, input to and responsibility for the communication process should be shared (Barnthouse et al., in press).

Local implementation groups would be charged with devising plans to implement one or more regional objectives at the local level. Like the regional planning entities, these groups should consist of representatives of interested parties or stakeholders. the general public, and technical experts. However, the members of this group would be individuals who are closer to the problem. That is, they could include industrial waste managers, members of community environmental groups, local officials, and local resource harvesters, rather than representatives of trade groups, national environmental organizations, and a Governor's office. They would use their knowledge of the local environment, waste generating processes, natural resources, and political economy to generate a plan for meeting the objectives in a manner that is least costly, least socially disruptive, and most effective. The plan would then be implemented by the governmental bodies, industries, and nongovernmental organizations participating in developing the plan.

In some cases (as with WSCAC), the system might work from the inside out (Fig. 1) rather than the top down as just described. Local groups may perceive a problem that they believe is larger than the scope of their authority. Alternately, they may have been given objectives that they believe cannot be met at their level. In such cases, they may push the problem "out" to the national government, state government, or other governmental body through such traditional mechanisms as proposed legislation. In other cases it would be more appropriate to work through a regional planning entity that could propose objectives and coordinate activities of local groups.

Scientists play an educational and advisory role in this scheme. Each of the entities must have sufficient understanding of the relationship between the needs of people and the functioning of the regional ecosystem to devise realistic and efficacious goals, objectives, or implementation plans. In addition, each stakeholder group must have sufficient understanding of ecosystem functioning over the long term and over large scales to develop positions that reflect their long-term interests. This educational function must not be seen as equivalent to an adult education course. The educational role of scientists grades into an advisory role. One of the important lessons learned by environmental scientists is that all actions have unintended consequences. It is necessary, therefore, for managers of environmental resources to engage in an adaptive management process that monitors the environment and indicates when plans must be changed to reflect the reality of system response.

Examples of biologically based strategies for institutional arrangements

An example of a creative initiative extending from the international to the local level is the Biosphere Reserve concept developed within the Man and the Biosphere Programme (MAB) of the United Nations Educational, Scientific, and Cultural Organization (UNESCO). Originally when developed in 1974, the Biosphere Reserve concept was aimed at the "conservation of natural areas and the genetic material they contain." Recent discussions have emphasized that local populations have a constructive role to play and human utilization should not be excluded from the Biosphere Reserve concept (UNESCO 1986). Batisse (1986) has argued that currently a biosphere reserve has three basic foci: conservation and protection of natural areas; research of international significance; and development of problem-oriented research, demonstration, education, and local participation programmes.

Each biosphere reserve includes one or more core areas strictly protected and consisting of typical samples of natural or minimally disturbed ecosystems. The core areas are normally surrounded by a buffer zone, strictly delineated and often corresponding to a single and autonomous administrative unit. The core areas and the buffer zone are surrounded by a transition area that constitutes a protective buffer, often not strictly delineated and corresponding more to a biogeographic than to administrative limits (Batisse 1986).

In the late 1980s, greater emphasis was placed on the role of humans (particularly local groups) in biosphere reserves. Starting in 1991, efforts have been underway to develop a research network synthesizing information available from biosphere reserves in 30 European countries, Canada, and the United States called the Biosphere Reserve Integrated Monitoring (BRIM) program (U.S. Man And the Biosphere 1993). The biosphere reserve concept is an example of an EMSA developed by scientists to protect globally significant areas: those biosphere reserves that have been most successful have included local personnel in the planning and implementation of projects. Over the last decade, the Unesco MAB office in Paris has worked diligently to include slides, videos, diskettes, and (or) CD ROMS to accompany books or articles developed for training purposes.

The RAMSAR Convention

The Convention on Wetlands of International Importance especially as Waterfowl Habitat, also known as the Ramsar Convention from its place of adoption in 1971 in Iran, is an international treaty (Table 3) providing the framework for international cooperation for the conservation of wetland habitats. Because wetlands are important in ecological processes as well as for their rich flora and fauna, the broad objectives of the convention are to stem the loss of wetlands and to ensure their conservation. To meet these objectives, the convention places general obligations on Contracting State Parties relating to the conservation of wetlands throughout their territory and special obligations pertaining to those wetlands that have been designated in a *List of Wetlands of International Importance* (Ramsar Convention Bureau 1987).

The Convention takes a broad approach in determining the "wetlands" that come under its aegis to include "... areas of

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marsh, fen, peatland, or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine waters, the depth of which at low tide does not exceed six metres." In addition, the Convention provides that wetlands "... may incorporate riparian and coastal zones adjacent to the wetlands and islands or bodies of marine water deeper than six metres at low tide lying within the wetlands." The Convention thus includes rivers, coastal areas, and even coral reefs.

Meetings of the Contracting Parties provide an opportunity for presentation and discussion of special reports such as one including a definition of wise use of wetlands. After deliberations and slight modification this definition that "... wise use of wetlands is their sustainable utilization for the benefit of humankind in a way compatible with the maintenance of the natural properties of the ecosystem" (Ramsar Convention Bureau 1987) was adopted by the Parties to the Ramsar Convention (Hollis et al. 1988). This Convention, while written and administered on the international level, encourages involvement of resource managers at the national level, and encourages on-site interaction between wetland scientists and local managers. Clearly, the Convention has scientific, educational, and communications components (Fig. 1).

The Sustainable Biosphere Initiative

In response to requests from scientific and legislative entities throughout Washington, D.C., the Ecological Society of America (ESA) undertook an extensive process of consultation and self-examination within the scientific community to establish research priorities for the future. Lubchenco et al. (1991) encouraged research in three areas: the role of living organisms in global change, biological diversity, and sustainable ecological systems. In addition, key research topics that cut across the three priority areas included (1) advance, test, and apply ecological principles for the design and use of sustainable, managed ecological systems at appropriately large scales and (2) accelerate the science of restoring damaged and degraded ecological systems by developing, testing, and applying principles of restoration ecology.

A Sustainable Biosphere Initiative (SBI) Project Office has been operating in Washington, D.C., since January 1992. With funding from several U.S. federal agencies, the office has been staffed by three full-time professionals. To date, SBI office staff have provided technical advice to various federal agencies and environmental organizations throughout Washington, D.C. (Haeuber and Cirillo 1994). Those who originally created the office had envisioned that an SBI office could play a critical role by informing managers and decision-makers of key emerging issues that have been identified by the ecological community, as well as by facilitating constructive dialogue between scientists and natural resource managers. When analyzing the initial, strong, positive response to SBI, the role of the news media in disseminating information about SBI should not be ignored (Holland 1994).

Here is a case of an EMSA that was broadly written by scientists eager to share ecological knowledge with stakeholders at the national level in particular.

The Pacific Rivers Council

An Ecosystem Management Strategy group may be particularly concerned about restoring the integrity of streams and floodplains in a watershed. The Pacific Rivers Council (PRC) is a private, nonprofit, environmental organization based in Oregon that has launched a major effort to restore degraded stream systems throughout the United States (Doppelt et al. 1993). The PRC had been organizing canoeing trips for years, and staff had become increasingly concerned with habitat degradation along many favorite canoeing courses. The PRC report to the U.S. Congress entitled *Entering the Watershed: A New Approach to Save America's River Ecosystems* calls for a strategic national community- and ecosystem-based watershed restoration initiative. In preparing their report, PRC staff worked closely with stream ecologists and limnologists to develop recommendations that were based on sound science and widely accepted ecological principles.

The EMSA proposed here represents an example of an environmental organization asking the scientific community for assistance in developing a workable strategy. The PRC report recommends a new approach to protect and begin to restore America's riverine systems and biodiversity through a Rapid Biotic and Ecosystem Response (RBER) approach. The approach involves three interconnected components, based in part on previous work (Seddell et al. 1991): (1) a comprehensive identification and protection of the remaining relatively healthy headwaters, biotic refuges, riparian areas, and floodplains: (2) following the protection of these areas, restoration can begin, focused initially on reducing or eliminating the threats to the remaining healthy areas; and (3) active participation of local communities and citizens in implementing the steps, through support for ecologically sustainable economic development. These recommendations grew out of discussions among 15 ecological scientists to determine a basic set of common ecological principles governing riverine systems, then legal experts reviewed current U.S. legislation, and discussions followed with representatives of the private conservation community. The resulting set of recommendations is aimed at riverine ecosystem protection on the national level and includes scientific, communications, and educational components. In this case, a document developed by an environmental organization, based on widely accepted ecological principles, has been used as a discussion tool with many U.S. legislators.

The Sustainable Biosphere Project

International cooperation and scientific exchange on environmental problems is also fostered among scientists from different countries through programs developed by the Scientific Committee on Problems of the Environment (SCOPE). One such program, which grew out of the ESA Sustainable Biosphere Initiative, was launched in 1992. The objective of the Sustainable Biosphere Project (SBP) is to build and make widely available an analyzed information base describing management policy and practice options that will result in sustainable ecosystems. Each of these options will be based on a synthetic analysis of ecological, economic, social, policy, and resource-management knowledge to examine selected integrated regional units of the Earth, thereby to assess successes

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and failures of managing sustainable systems (Mooney and Sala 1993). For each region, disciplinary experts will summarize and analyze the ecological, geographical, cultural, economic, political, legal, and social aspects and information available. Local experts will evaluate whether current patterns and strategies for using and managing regional resources can be sustained over the long term and the relevant costs. These commissioned studies and analyses will provide the initial knowledge base for regional case study workshops (SCOPE 1993).

During the first two steps (developing an analyzed information base and describing new management practice and policy options) existing gaps in the knowledge base will be identified, then summarized, and workshop participants will identify those that require the highest priority for attention. Also, recommendations will be made identifying possible research approaches to be used in filling each of these information gaps and about potential research collaborators from the region and elsewhere in the world. To meet this objective, seven case studies will be conducted in the following integrated ecological–geographical systems: Amazon Basin, Baltic Drainage Basin, North American Great Lakes Drainage Basin, Himalayan – Hindu Kush Mountain Drainage Basin, Mediterranean Basin, Oceania Island System, and Southern African Savanna System. These seven systems were selected because they represent a known, definable set of interactions among ecological, social, and economic conditions; an adequate data base from which to propose management options exists; each region contains a range of administrative and cultural systems used for managing natural resources; and each region involves more than one country. The hope for SBP is that it will produce tools for ecologically sustainable resource management, including formal publications, working data bases, tools, educational presentations, and new links between disciplines and groups (SCOPE 1993). Here is an example of an evolving project that includes local experts and that is focusing from the outset on having a multidisciplinary approach to development of management plans, interactive computer programs, and various public communication materials.

The Environmental Monitoring and Assessment Program

Another example involves the U.S. Environmental Monitoring and Assessment Program (EMAP). In 1988, the U.S. Environmental Protection Agency's Science Advisory Board recommended implementing a program to monitor ecological status and trends for identifying emerging environmental problems before they reach crisis proportions. In the following year, the Administrator of EPA established an agency priority for the 1990s to confirm that the Nation's annual expenditure on environmental protection is producing the intended results toward maintaining and improving environmental quality (Reilly 1989). In an effort to identify environmental problems before they become irreversible and to allow the evaluation of regional and national progress toward achieving environmental goals, EPA's Office of Research and Development (ORD) began planning the EMAP. Initiated in 1989, EMAP was created to monitor and assess the condition of the Nation's ecological resources, thereby contributing to decisions on environmental protection and management by identifying the extent, magnitude, and location of large-scale environmental problems.

EMAP is designed to provide information needed to quantify the current status and trends in the condition of the Nation's ecological resources and (to the degree feasible in a monitoring program) information needed to diagnose why those conditions might exist. EMAP was originally designed as an interdisciplinary, interagency research, monitoring, and assessment program with the following objectives (Thornton et al. 1993): (1) estimate the current status, trends, and changes in selected indicators of the condition of the Nation's ecological resources on a regional basis with known confidence; (2) estimate the geographical coverage and extent of the Nation's ecological resources with known confidence; (3) seek associations between selected indicators of natural and anthropogenic stresses and indicators of condition of ecological resources; and (4) provide annual statistical summaries and periodic assessments of the Nation's ecological resources. To meet these objectives, EMAP has been developing social values based indicators of the condition of ecological resources and of natural and anthropogenic stressors influencing this condition. The indicators must be compatible with EMAP's rather unique monitoring design to permit quantitative and unbiased estimates of ecological status and trends, analysis of associations between indicators of ecological condition and environmental stress, and sufficient flexibility to accommodate sampling of multiple resource types (Barber 1994).

At present, EMAP is at a crossroads. Lack of continuity in program management and insufficient resources to fully implement the program have led to proposed revisions for an EMAP Phase II (Messer, in press). A desire on the part of the U.S. Administration to see federal agencies work closely together on a single environmental monitoring and assessment program, combined with budget constraints, have led to the formation of an interagency effort under the leadership of the White House Office of Science and Technology Policy to develop a combined federal effort to implement a more effective environmental monitoring program for the United States. Within this larger interagency effort, EPA's current Assistant Administrator for Research and Development has directed the next phase of EMAP to design and evaluate a scientific approach that integrates research results from intensive field sites with those from more conventional monitoring by federal and state agencies (memorandum from Robert Huggett dated 12 October 1995). Given the changes in political pressures (both internal and external to EPA) with which EMAP has had to cope over the last 6 years, along with shrinking budgets for all U.S. federal agencies, the streamlining and coordinating effort currently underway through the White House Office of Science and Technology Policy appears to be the most logical way to achieve EMAP's original objectives.

Summary

Three of the seven programs (Table 2) have been in existence for over 15 years, while four are relatively new "developing" programs. The most successful programs maintained an active effort to communicate effectively. (1) I propose that governments within a geographic area set up strategies to manage human activities within ecoregions to accomplish particular

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goals. Such EMSAs are envisioned as setting goals at a national or regional level, developing regional objectives, and initiating and overseeing the development of implementation plans at local levels. (2) The examples (Table 2) provide strategies and agreements that plan for the long term, rather than 1 year at a time. (3) A successful EMSA will include direct involvement of local elected officials, effective communication among all parties (including the news media and legislators), a holistic approach to the management question, a basis of sound science, and engagement of a blend of talents. (4) Effective and efficient solutions to environmental problems are best developed by involving natural and social scientists possessing knowledge of fundamental principles in their respective disciplines with local stakeholders who understand both the local resources and the users of those resources. (5) Coalitions of regional environmental planning and management bodies should be organized to share information and experience, so that successes in one region may be applied elsewhere.

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Considerations of scale in habitat conservation and restoration

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Abstract: Space and time function together to shape communities and ecosystems. As a result, the definition of scale of observation is critical to the design of successful habitat conservation and restoration strategies. Traditionally, aquatic habitat studies were focused on small spatial and temporal scales such as a stream site or reach. Present challenges for managers of large systems such as the Great Lakes include dealing with a variety of stresses acting together at different spatial and temporal scales and understanding how fragmented patches of habitat interact to create ecological change at a larger scale. The design of effective habitat management strategies will require increased attention to the scale-related problems presented by large systems. These problems include the appropriate scale of observation relative to habitat management objectives, the linkages among habitat structures and processes, the need for comprehensive baseline studies, and monitoring at multiple scales. New methods for dealing with these problems, particularly on lake systems, are required. Long-term financial commitment within agencies, and collaboration among agencies that share management responsibilities for habitat will assist in addressing these scale-related issues.

Résumé : Le temps et l'espace modèlent les communautés et leurs écosystème, c'est pourquoi la définition d'une échelle d'observation est liée si étroitement à la conception des stratégies de protection et de rétablissement des habitats. Avec l'approche classique, on étudie les habitats aquatiques à des échelles réduites d'espace et de temps, comme un tronçon d'un cours d'eau ou une station. Les aménagistes de vastes écosystèmes comme les Grands Lacs doivent apprendre à jongler avec une variété de facteurs de stress aux effets synergiques, mais qui s'exercent à différentes échelles temporelles et spatiales. Ils doivent aussi trouver de quelles façons des habitats fragmentés interagissent pour modifier des écosystèmes à une échelle supérieure à la leur. Pour concevoir des stratégies efficaces de gestion des habitats, il faudra porter davantage attention aux problèmes d'échelle associés aux grands écosystèmes. Ce sont notamment la bonne échelle d'observation à choisir au regard des objectifs d'aménagement, les liens entre les mécanismes et les structures des habitats, la réalisation d'études de référence complètes et les opérations de surveillance à différentes échelles. Il faut inventer de nouvelles façons de traiter ces problèmes, particulièrement dans le cas des écosystèmes lacustres. Les engagements financiers à long terme des organismes responsables de l'aménagement du territoire et la collaboration sont des éléments de réponse à ces problèmes.
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Introduction

The Great Lakes, characterized by their very large surface areas, complex biological communities, massive physical and biological changes, and functional and physical links to the surrounding watersheds, present enormous challenges for resource managers. Such challenges include setting habitat objectives to support desired biological communities, monitoring the status of habitat, determining best protection and restoration methods, and evaluating the success of those methods. Choosing the appropriate scale for such activities is an essential, yet commonly overlooked, requirement.

In recent years, resource managers have increasingly realized that site-level mitigation of habitat effects often has not achieved the desired results at the population level. Broader scale management actions are required to manage human interaction with aquatic systems (White 1996).

We reviewed HabCARES contributed papers to focus issues of scale in habitat conservation and restoration, and to identify what is needed to incorporate the scaling problem into Great Lakes habitat management activities. We adopted the

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following definitions: (1) "Scale" refers to the temporal and spatial dimension of an object or process. Large scale requires observation and (or) action over relatively long periods of time, across large parcels of space, or both (Allen and Hoekstra 1992). Scale is characterized by both grain and extent (see below). (2) "Grain" is the finest level of spatial or temporal resolution; that is, the limit of the resolving power of individual measurements. Grain determines the smallest and most ephemeral entities that can be found in the data (King 1990; Allen and Hoekstra 1992). (3) "Extent" is the size or duration of the study or the spatial and temporal dimension of the data. If the size of the entity is larger than the spatial extent of the data collection, then phenomena associated with it cannot be observed. Similarly, if the temporal framework of the study is too short to include a full cycle of a process, then phenomena associated with these temporal extents cannot be seen.

Why is scale important in habitat management?

Ecological processes and structures are multiscaled. The structures and processes observed in ecosystems show properties at a variety of scales, and both respond to perturbations that may be naturally or anthropogenically induced (Harris 1994). The dimensions encountered by stream ecologists extend over 16 orders of magnitude in both time and space (Minshall 1988). For example, spatial dimensions extend from dissolved and colloidal organic and inorganic matter to the biosphere (Minshall 1988). Any interaction between ecosystem components (such as fish and their habitat), therefore, implies a relation between different time and space scales. For example, the changes in stream sediment load caused by a localized streambank disturbance occur at smaller spatial and temporal scales than do changes associated with watershed deforestation. Further, the interaction between such habitat disturbance and stream biota depends in part on the temporal and spatial scales associated with the life history of the organisms themselves. Cunjak (1996) shows that, to account for the range of movement and habitats associated with stream fishes in winter, a large scale of study is necessary.

Space and time function together to shape communities and ecosystems. Their interaction may occur at a variety of scales from short term and local, to evolutionary and global. Aquatic habitats undergo changes in time and space, ranging from small to large scale and from gradual to catastrophic (Crowder et al. 1996). Small-scale changes include shoreline activities such as localized dredging, while large-scale changes include climatically controlled changes in lake levels. Cattail beds in the Kingston Basin of Lake Ontario gradually enlarged with decreasing water depth, while macrophytes suddenly collapsed when algal shading reached a threshold (Crowder et al. 1996). Communities and ecosystems are transformed or sustained as a result of such processes acting together at a variety of scales.

Aquatic systems undergo natural disturbances at various scales. Overlaid on this pattern of natural disturbance is a variety of human-induced disturbances that may not operate at the same temporal and spatial scales as natural disturbances (Resh et al. 1988). Thus, both land use and physiography can be the major determinants of biotic patterns in systems (Rabeni and Sowa 1996).

As a result of the multiscaled nature of ecosystems, the definition of the scale of observation is critical. Our perception of ecosystem characteristics and dynamics, such as change to habitat quality or quantity, is dependent on the scale of observation, both grain and extent. Different extents encompass different components and interactions, and observations of different grain will resolve different components, interactions, and dynamics (King 1993). Observations in a small bay over 1 yr will lead to a different system description than will observations over the entire lake and several decades (Allen and Hoekstra 1992). Similarly, fine-scale, medium-scale, and large-scale observations of stream characteristics provide different descriptions of fish habitat (Cunjak 1996; Rabeni and Sowa 1996; Richards et al. 1996). Microhabitat variables such as water velocity, depth, proximity to cover, and substrate type are often used to construct habitat suitability index curves. Medium-scale habitat characteristics, measured at the riffle, run, or stream-reach scale, indicate the variety of microhabitat conditions available. Landscape-scale considerations of habitat take into account large-scale movements of fish and effects of physiographic variables and land use.

In designing a program to achieve habitat restoration or to monitor change, therefore, choice of time and space scale are of overriding concern. The scale of observation chosen exists within a hierarchy of scales, and once the initial entity of interest is determined (e.g., stream reach, whole lake), the organizational hierarchy will be defined (Pickett et al. 1989). Determination of the major issue and entity of concern leads to both the choice of scale appropriate to the entity and to the hierarchical structure or context of the entity. This process of moving from issue to entity to scaling to hierarchical organization is the key approach to defining the management context (J. Imhof, Ontario Ministry of Natural Resources, P.O. Box 5000, Maple, ON L6A 1S9, Canada, personal communication). As our focus shifts to higher levels of organization, disturbances may be included in, and masked by, the normal dynamics of the higher level entity (Pickett et al. 1989). Ryder and Kerr (1989) suggest that at small scales and within simple biotic complexes the problem of system definition can be "a relatively relaxed matter," but as spatial scale increases, so do the opportunities for environmental noise to mask the behaviour of the system of interest. This is particularly true in large-scale systems like the Great Lakes (Kelso et al. 1996) and may explain in part why scale issues have been more explicitly addressed in work on stream tributaries than in lakewide habitat management.

Past and present practice

Although there are compelling reasons to clearly determine the appropriate scale of observation for habitat management, assessment, and monitoring, there are not many examples on the Great Lakes where this has been done. In general, ecosystem science is probably limited by the fact that traditional ecological studies have taken place on very small temporal and spatial scales (Woodley 1991). There have been relatively few long-term, large-scale studies. Thus, we understand a lot about organisms, less about populations, and little about communities and ecosystems. More recently the recognition that many ecological problems are large scale has led to a gradual shift away from the traditional small-scale approach. Work on global cli-

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mate change (Schindler et al. 1990) and long-range transport of atmospheric pollutants (Håkanson et al. 1990, 1992; Neary and Dillon 1988) are notable examples.

The problem of choosing an inappropriately small scale of observation is particularly true of studies of fish habitat, where science is still largely in the autecological descriptive stage. Most attempts at habitat restoration have been at the autecological level, with habitat "constructed to provide shelter, concentrate food organisms, or increase reproduction of a target species" (Ryder and Kerr 1989). Seldom have managers looked for a net gain in terms of increased standing stock of desired species over time, as long as a local and (or) short-term benefit has been observed.

One reason for this small-scale focus for habitat management may relate to our understanding of habitat and its link to populations. Scientists and managers may share an understanding of the meaning of "habitat" at small scales: the variety of physical and structural features believed to be important to animals and associated with a particular life activity or requirement (spawning, nursery, refuge habitat) (Kelso et al. 1996). The meaning of habitat at a larger, ecosystem-level scale is more nebulous, being linked in some way to ecosystem "integrity" or "health." Again, this points to the need for a hierarchical context for how we view issues and possible solutions to them.

There are additional reasons for our historically narrow perspective on fish habitat. Stream habitat management has traditionally occurred at small scales, because streams are small enough to be manipulated, the channel is readily seen to be where the fish live, and broader watershed work is made more difficult by the fact of multiple ownership and competing land uses (White 1996). Where studies have been implemented at the watershed or landscape scale, they have primarily focused on how watershed-scale parameters relate to water chemistry. Often, managers do not recognize the importance that watershed features play (e.g., extent of upstream wetlands, dominant surficial geology) in determining the composition of fish and invertebrate assemblages at stream sites or reaches. Relatively few studies have investigated the relationship between watershed features and biological communities (Richards et al. 1996). Finally, our past focus on small-scale habitat management may be caused by the fact that humans are visual animals. We define an issue, problem or condition within the context of what we can visually take in. Therefore, we tend to bound problems within the context of our "point of view," or what is easily observable.

Failure to carefully consider the scale of observation is a common limitation to population and habitat studies. In many cases, analysis to develop a solution to habitat problems is done without due regard for the scale conditions above and below the feature scale being examined. Restoration projects in the Great Lakes Basin have often failed because problems were being manifested and solutions designed at smaller spatial or temporal scales than those required. Physical habitat restoration on streams has most often been attempted at the site or reach level, while causes are related to changes in the watershed (Imhof et al. 1996). For example, land-use practices have led to massive changes in Great Lakes watersheds through agriculturalization and urbanization; these have been shown to effect major changes to fish habitat and populations (Evans et al. 1996). In another example, Richards et al. (1996) showed that, although the presence of woody debris in stream channels is most strongly related to local riparian characteristics, channel morphology is more strongly influenced by whole watershed characteristics that dictate hydrologic conditions. Management or creation of narrow riparian buffer strips along streams may help with the addition of woody debris to stream channels but may have little influence on many aspects of stream channel morphology that influence fish and invertebrate distributions.

Similar problems can be seen in the choice of temporal scale for habitat work. We need to understand habitat requirements throughout the life history of the species of interest to set specific quantitative conditions required for habitat restoration (Casselman and Lewis 1996). Static habitat assessment cannot allow the observer to view the responses of populations to changes in habitat supply. Habitat demand is a dynamic result of the constraints that density-dependent mechanisms impose on fish populations (Minns et al. 1996). Without the results of dynamic assessment, our conclusions about habitat limitations are based on a combination of point-in-time evaluation of single life stages and intuition and may lead us to misplaced priorities for habitat protection. Minns et al. (1996) demonstrate this clearly for northern pike (*Esox lucius*) in Hamilton Harbour. Their model suggests that, contrary to our intuition, fry and juvenile–adult habitats are more limiting than are spawning habitats.

One challenge facing Great Lakes managers is to understand and address the large number of different stresses acting on fish populations and habitats. These stresses operate at different spatial and temporal scales. For example, prevailing strategies for restoring Lake Erie may not be directed at the most important stresses. Pollution-limitation strategies have received the most attention, yet changes in species composition indicate that destruction of the nearshore, tributary, and wetland habitats through land use has played a major role (Koonce et al. 1996). Failure to acknowledge the relative contributions of these stresses is a scale-related problem.

Habitat restoration strategies are most often developed to help achieve fish population or community objectives. Monitoring programs to assess the success of habitat restoration strategies must be linked to those population or community objectives. Several papers at this workshop addressed the importance of particular habitat variables at specific life stages (Cunjak 1996; Evans et al. 1996; Geiling et al. 1996; Gunn et al. 1996; Hayes et al. 1996). However, the ultimate test of whether habitat is limiting must be measured in terms of a population-level response. This test most often requires a large-scale study, yet few investigators have set out to determine the temporal and spatial scale required to detect changes in fish abundance and thus test the ultimate success of habitat conservation and restoration strategies. Lester et al. (1996) estimate that, for nearshore species in inland lakes, the time scale for a study designed to detect a twofold change in population abundance is greater than many present studies (7 yr before and after the change).

Designing more effective strategies

We recommend a number of areas where resource managers need to focus their efforts for more effective habitat management strategies with due consideration of scale issues.

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Scale of observation and action

Managers of Great Lakes habitat need to begin with a fundamental choice of scale: what scale is relevant in collecting information to (1) diagnose a problem, (2) identify a specific need for habitat restoration, (3) determine the extent of restoration required in both space and time, and (4) evaluate the success of restoration efforts? Does the required scale of study vary for each of these steps?

Habitat protection and restoration should be guided by ecosystem targets and their associated indicators (Kelso and Hartig 1995; White 1991). Once the targets are established, managers must be able to measure progress toward them. This requires measures chosen at the appropriate temporal and spatial scales. Ryder and Kerr (1989) argue that we must address habitat needs in a hierarchical perspective, beginning at the ecosystem level. This broad perspective then focuses habitat in its most fundamental and all-embracing role, as a centre of organization (Steedman and Regier 1987) and allows the determination of what habitats are limiting in space or time. Because the hierarchy of habitats can be considered spatially nested, a stress at one scale can affect all smaller scales. For example, changes in hydrology at the watershed level will impact on the stream reach and site level; attempts to reestablish habitat at the scale of individual sites will be unsuccessful until larger scale hydrological causes have been rectified. Therefore, management will be most successful if it addresses the largest scale at which the stress occurs (Rabeni and Sowa 1996).

It is clear that stress reduction should be implemented and evaluated at scales appropriate to the scale of perturbation, while the effectiveness of rehabilitation efforts should be gauged by the response of whole ecosystems (Kelso et al. 1996). In the Great Lakes context, restoration can be most effectively accomplished by management action at the regional, rather than local, scale. This is because fish communities appear to be related primarily to regional and biogeographical factors (Kelso and Minns 1996). A large-scale approach to habitat management will also allow for the natural movement of habitat types through space and over time (Crowder et al. 1996).

Sometimes small-scale actions are all that is available while we work towards resolution of larger scale problems. Lacroix (1996) demonstrates that the small-scale application of limestone to streambeds and spawning sites for Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) can be used to mitigate the effects of low stream pH and increase survival and productivity at individual sites. Yet ultimately, catchment treatments may be more effective (Howells and Dalziel 1991), and it is pollution abatement in the whole catchment that is having major improvement effects on the degraded lakes of the Sudbury Region (Keller and Gunn 1995).

Linkages

To effectively manage habitat, we require an understanding of linkages operating both within and among scales. These linkages must be understood in the context of existing or potential human-induced changes to natural disturbance patterns. An additional challenge is to determine how fragmented patches of habitat, some being exposed to a disturbance, others free from disturbance, and still others recovering from earlier damage, interact to create ecological change at a larger scale. This requires an understanding of the dynamic linkages between biological and physical processes that may critically interact to define recovery potential. The dynamic nature of habitat that is evident in the Kingston Basin of Lake Ontario points to the importance of understanding how habitats naturally change in time (Crowder et al. 1996). This dynamic nature of ecosystems is what must be restored and protected, not simply individual ecosystem components (Doppelt et al. 1993; White 1996). Likewise, the structural and functional linkages among species must be understood and accounted for in planning restoration initiatives. The traditional approach of targeting a single species in habitat restoration is a narrow perspective that ignores the links that may cause the system to respond beyond the target species (Minns et al. 1996). Finally, the biophysical and chemical linkages between terrestrial and aquatic systems must be understood (Richards et al. 1996).

Baseline studies

Quantification of the effects of habitat manipulation is difficult unless there is baseline knowledge of the state of major environmental determinants (Ryder and Kerr 1989). A broad environmental assessment is required before habitat rehabilitation is attempted (Ryder and Kerr 1989; Crowder et al. 1996; Richards et al. 1996).

Multiple-scale studies

Given the nature of agency objectives for the Great Lakes (Hartig et al. 1996; Kelso et al. 1996; Koonce et al. 1996), we suggest studies that focus on adult fish abundance are most appropriate for diagnosing a habitat problem and evaluating the success of rehabilitation efforts. Such studies are also likely to offer the most efficient returns in terms of sampling cost. Substantial effort might be invested in studying the effects of habitat changes on earlier life stages, but these efforts are wasted if the effects are not manifested as changes in adult abundance. Perturbations that affect early life stages are attenuated as they are transferred to the larger extent and longer time scales of later life stages. The final life stage (i.e., adult) can be viewed as a natural integrator of scale.

Fine-scale studies of earlier life stages and (or) specific habitats become useful when adult abundance is known to be affected, because studies at this scale may identify critical factors and indicate what habitat restoration is needed. Thus, larger scale measurements focussing on adult fish abundance and environment may need to be complemented by finer grain measurements. Because stresses are acting at both local and regional or even whole-lake scales, rehabilitation and restoration efforts at these scales should be complementary to be more effective (Kelso et al. 1996). In this sense, for any scale of observation, it is necessary to look both to larger scales to understand the context and to smaller scales to understand the underlying mechanism (Imhof et al. 1996). Such a hierarchical approach to examining fish–habitat relations offers the most comprehensive view of ecological systems (Rabeni and Sowa 1996) and provides a mechanism for quantifying watershed and stream interactions (Richards et al. 1996).

Woodley (1991) describes four approaches to monitoring: (1) reductionist, (2) threat specific, (3) hypothesis testing, and (4) integrated monitoring to measure the emergent properties of the system. He argues that only the last of these approaches attempts to account for differences in spatial and temporal

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scale and, therefore, holds the most potential for ecosystems. Integrated monitoring incorporates stress ecology, landscape ecology, biological indicators, and conservation biology. However, the integrated approaches are not yet well developed.

New methods

Theoretical models that incorporate multiple scales are needed to guide the collection and interpretation of data. The hierarchical models proposed by Imhof et al. (1996) and Rabeni and Sowa (1996) are a step in this direction. The model proposed by Imhof et al. (1996) deals primarily with spatial scale; their basic framework could be readily used to examine temporal factors as well. The model specifies measures at four levels within a watershed (site, reach, physiographic unit, and watershed), and the authors discuss how information at various scales could be integrated to develop land management strategies. Similarly, Rabeni and Sowa (1996) propose a hierarchical approach to separate those habitat conditions responsible for presence and abundance of a species from those conditions responsible for within-stream distribution. Richards et al. (1996) demonstrate the use of a hierarchical approach to examine the relative influences of management-related (e.g., land use) and fixed (e.g., surficial geology, land form) watershed characteristics on stream habitats and biota. These developing approaches tend to be focused on stream systems, where hierarchy theory is perhaps more readily tested. New approaches for lake environments are needed.

The multiscaled nature of ecosystems, and the stresses acting upon them, presents a major theoretical and practical challenge. The use of hierarchical approaches for examining spatial and temporal fish habitats promises to provide an avenue for developing cost-effective fisheries management techniques. However, continued investigations of this nature will often require the utilization of large spatial data bases that have not been extensively utilized by fisheries managers because of computational difficulties or lack of access. Fortunately, many spatial data bases relating to geological, hydrological, and land-use characteristics of Great Lakes watersheds and coastal regions are becoming available in digital form that can be rapidly stored and manipulated in geographical information systems. The techniques for integrating these data bases to help address fish habitat questions are being developed. As government and private sector geographic data bases become available, our ability to look for and identify relationships across various scales will increase (Richards et al. 1996).

Agency collaboration

Large-scale monitoring of habitat and implementation of effective restoration strategies requires an increased commitment to interagency collaboration at all stages from objective setting through design and implementation. Watershed initiatives are an inland example of integrative studies on larger scale landscape units. Lester et al. (1996) recommend the study of several lakes at relatively low sampling intensity to evaluate the effects of habitat alteration. On the Great Lakes, this approach might be followed using a variety of sites (AOCs, basins) across a lake or lakes. Such an approach would require institutional coordination and commitment in exchange for more cost-effective programs in total. Perhaps even more importantly, individual agencies will need to make the long-term financial commitment to monitoring the abundance of Great Lakes fish populations as a broad-scale indicator of habitat conservation and restoration strategies.

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Assessing the ecological effects of habitat change: moving beyond productive capacity[1]

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Abstract: Productive capacity can be defined as the "ecological effect" end of a habitat change → ecological effect cause–effect pathway. Determining whether and how a habitat manipulation, either inadvertently or deliberately, will affect productive capacity is the key analytical step of habitat management. We describe a process to ensure that this step is conducted in a manner that is rigorous and relevant. The process has four components: (1) determination of management objectives, (2) identification of indicators, (3) analysis of cause–effect pathways linking habitat changes to ecological effects, and (4) determination of strategies to effect desirable habitat change. The core of the process is the third step, in which we propose the use of hypotheses-of-effect, a network of cause–effect linkages leading from habitat change to ecological effects, to ensure rigorous assessment of possible effects. We illustrate the process using examples of timber management effects on migratory brook trout (*Salvelinus fontinalis*) and urbanization effects on littoral warmwater communities. We argue that this process, in addition to providing a rigorous means of assessing the evidence relevant to a particular issue, also provides an effective tool for examining uncertainty. We advocate the adoption of this process by management agencies as a method for adaptive habitat management.

Résumé : La capacité de production peut être définie comme l'«effet écologique» final résultant d'une modification de l'habitat, c'est-à-dire le résultat d'un processus de cause à effet. La principale étape d'une analyse de la gestion de l'habitat consiste à déterminer si et dans quelle mesure une modification de l'habitat, délibérée ou non, aura un effet sur la capacité de production. Nous décrivons une méthode permettant d'assurer que cette étape est menée de façon rigoureuse et pertinente. La méthode comporte quatre éléments : (1) la détermination des objectifs de gestion, (2) la détermination des indicateurs, (3) l'analyse des mécanismes de cause à effet qui s'exercent entre les modifications apportées à un habitat et les effets écologiques, et (4) la détermination des stratégies permettant d'apporter des modifications souhaitables à l'habitat. C'est le troisième élément de cette méthode qui est le plus important; nous proposons une série d'effets hypothétiques, c'est-à-dire un ensemble de causes liées à certains effets qui permettent de prédire les effets écologiques qu'entraîneront certaines modifications apportées à l'habitat, dans le but d'analyser de façon rigoureuse tous les effets possibles. Nous illustrons cette méthode à l'aide d'exemples: les effets de la gestion forestière sur les populations migratrices d'omble de fontaine et les effets de l'urbanisation sur les communautés vivant dans les eaux tempérées près du rivage. Nous sommes d'avis que cette méthode, outre le fait qu'elle constitue une façon rigoureuse d'évaluer les données dans un cas particulier, offre également un outil efficace pour évaluer l'incertitude. Nous proposons aux organismes de gestion d'adopter cette méthode pour une gestion adaptative de l'habitat.
[Traduit par la Rédaction]

Introduction

In 1986, the Canadian federal government released a policy for the protection of fish habitat (DFO 1986) whose purpose was to ensure the net gain of fish habitats in Canada. One of the key tenets of this policy is that the fundamental attribute of fish habitat to be protected (restored or enhanced in the case of compensation) is its productive capacity. Productive capacity is defined in the policy as "the maximum natural capability of habitats to produce healthy fish, safe for human consumption,

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or to support or produce aquatic organisms upon which fish depend." As with many integrative ecological concepts, the term productive capacity is ambiguous. This ambiguity is beneficial, as it allows the concept to be applied to the broad array of circumstances wherein habitat modifications may be affecting valued components of aquatic ecosystems. The price to be paid for this generality, however, is the challenge, for any specific situation, of determining how to quantify changes to productive capacity. The productive capacity concept and its enshrinement in policy begs two important questions: (1) how should productive capacity be measured and (2) how well do we understand the relationship between productive capacity and human-induced habitat change. These two questions are the subject of this synthesis.

Although the above definition of productive capacity derives from a Canadian policy document, its relevance to the science of habitat management transcends political jurisdictions. Many of the formative ideas underlying the development of the productive capacity concept stem from seminal works in fisheries science (e.g., Ivlev 1966; Ricker 1975). In a contemporary context, the concept seeks to provide a practically useful measure of habitat suitability, such that changes in its value can be ascribed to ecologically significant habitat change. Defining meaningful, measurable metrics of habitat loss (or gain) is a need basic to all agencies whose mandate includes the conservation and restoration of aquatic habitats.

The need for a process for measuring productive capacity

The term productive capacity suggests a relationship to two common concepts in ecology: (1) production or productivity and (2) carrying capacity. Both concepts have been defined in the ecological literature, but neither definition is adequate to capture the intended breadth of definition of the productive capacity concept. While a loss of ecological production is often the most important metric of the effect of habitat loss, especially for exploited fish populations, there are many instances in which production is not the attribute of interest. For example, a habitat manipulation may result in no change to overall production but a pronounced shift in species composition or diversity. Depending on the human values associated with the species inhabiting the affected system, the implications of change can range from inconsequential to important (i.e., loss of an endangered species). Even where stock productivity is of primary interest, production in exploited populations can be affected by the level of harvesting, irrespective of changes in habitat, implying that production itself may not be a sensitive, diagnostic, indicator of important changes to habitat. We interpret the spirit of the productive capacity concept to mean something more than production, something whose definition is issue dependent and something that constitutes the "effect endpoint" of the cause–effect pathway linking habitat changes to ecological effects.

While a broad definition of productive capacity may be necessary to embrace the breadth of concerns about habitat manipulations, it is certainly not sufficient to allow scientifically rigorous habitat management. In practice, this broad definition must be translated into a set of specific, measurable ecosystem attributes that can form the basis of both predictions about, and monitoring of, effects. Human activities alter fish habitats in innumerable ways, leading to a host of different effects on the fish populations utilizing those habitats. The changes can be to physical, chemical, biological (e.g., vegetation removal) aspects of a fish species' or community's habitat; can be direct (e.g., substrate removal) or indirect (e.g., land-use changes affecting hydrology); and can occur at a variety of different spatial and temporal scales. The effects of such changes could range from altered contaminant levels (edibility) in individual fish to shifts in species diversity. With such a diverse array of potential interactions all being part of the habitat change → ecological effect linkage, it is important to define a process to focus the investigation of a particular issue. This is a significant challenge, but we argue that it is essential to utilize such a process to ensure comprehensiveness, objectivity, and analytical rigour. In this paper we propose such a process and illustrate it using two examples relevant to the Great Lakes basin.

The overall process

Habitat management issues can be broadly divided into two groups. The first (type A) consists of issues where management objectives have been specified, and the question is whether habitat manipulations can be used to achieve the stated objectives. Great Lakes Remedial Action Plans (RAPs) contain good examples of type A issues, wherein habitat manipulations are considered as means to restore impaired uses (Koonce et al. 1996). The second (type B) includes cases where a particular habitat manipulation or set of manipulations is proposed, and the question is what the effects of the manipulations might be. Type B issues are frequently part of environmental assessments, where the manipulations are proposed to meet economic objectives (e.g., dam construction, urban development), and concerns have been raised about ecological effects. These two groups of issues are quite different, but they have (or should have) in common four primary components: objectives, indicators of ecological effects, the habitat changes themselves, and tools or strategies to achieve the habitat changes. Our process comprises the systematic evaluation of each of these components and the linkages among them.

The analysis of all habitat management issues should begin with a careful articulation of ecological objectives or targets. For type A issues this requirement is obvious. However, even in cases (type B) where the challenge is to judge whether the effects of an already proposed manipulation are desirable, or at least not deleterious, it is essential to determine objectives at the outset. Consider a simple, but realistic case in which a dam removal is proposed that will enhance access for migratory salmonine species to the headwaters of a river system (Giesy et al. 1994). The migratory species are not native and contain elevated body burdens of organochlorine contaminants. The headwater areas are presently occupied by a native, nonmigratory salmonine species and by mammalian and avian predators that feed on salmonines and presently have low organochlorine body burdens. Before one can judge the suitability of this manipulation, it is necessary to know the ecological management objectives for the area (e.g., enhancing migratory salmonine fisheries; conserving native species; eliminating man-made barriers to fish movements; minimizing the exposure of wild populations to toxic substances; minimizing access of other migratory species such as the sea lamprey

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(*Petromyzon marinus*) to new habitats). Regardless of the type of issue, the first step should be the specification of objectives or targets.

A clearly stated set of objectives is a prerequisite for the next step in the process: the determination of relevant indicators of ecological effects. The indicators are those aspects of the population, community, or ecosystem that provide a measurable reflection of whether objectives or targets are being met. The crux of habitat management is allowing or prescribing habitat changes that have desirable ecological effects and preventing or mitigating those changes that have undesirable effects. In our process, indicators provide the measures of productive capacity according to our earlier definition; they represent the endpoints of a chain of cause and effect that begins with habitat change. Beanlands and Duinker (1983) coined the expression "valued ecosystem component" to fulfil a similar purpose in environmental impact assessment. The essential attributes of the indicators are that they are measurable and that their measured state can be used to determine the extent to which the previously stated objectives are being met. Once these indicators have been determined, an important part of any habitat management study is to design and implement a procedure for assessing the current status of the indicators, a benchmark against which future change can be contrasted.

The third component of the process is the list of habitat changes to be considered. For type A issues one needs to consider what habitat change might influence the indicators. For type B issues the habitat changes have already been specified, as in our dam example above. The rigorous, analytical component of the process centres around systematically evaluating the evidence for linkages between the habitat changes under consideration and the indicators of ecological effects; we describe the steps in detail below. As the analysis proceeds, the appropriate scale for assessing these influences needs to be specified (Lewis et al. 1996). Modifications to habitat fundamentally have two components: the magnitude of change per unit area and the overall areal extent of the change (Minns 1995). To a large degree, the scale issue is one of emphasizing the importance of quantifying the second component (areal extent) when evaluating the overall effects of a habitat modification. Minns (1995) developed a quantitative methodology for integrating these components. As well, the relative influence of other factors on the indicators needs to be examined, including both habitat features that are not being considered for manipulation and processes other than habitat that affect the indicators (e.g., biotic interactions, exploitation). Failure to consider the contribution of these other factors to the dynamics of the indicators can easily lead to naive expectations for the effects of a particular manipulation when in fact some other ecosystem component is limiting. Finally, once the potential influence of the manipulation(s) has been evaluated in the proper spatial, temporal, and ecosystemic context, a strategy can be selected to achieve the objectives.

This process is not novel, nor does it embody any insights beyond what might be considered common sense. Similar approaches have been advocated for environmental impact assessment in Canada (Beanlands and Duinker 1983) and for environmental monitoring in the United States (EMAP 1994). Yet, despite its seemingly obvious nature, more often than not habitat management issues have been confronted without using a framework such as this. As a result, measures to protect or restore habitats have not adequately considered issues of scale, with the result that large-scale processes (e.g., watershed land-use changes) override the desired effects of small-scale manipulations (e.g., spawning site rehabilitation). Similarly, habitat manipulations may not have the desired effects because other processes (e.g., predation or a limiting habitat at another life stage) exert a greater control over the dynamics of the target species or community. Finally, the effects of the habitat alteration, even if they do occur, may not be observed because either inappropriate indicators were chosen, or inadequate commitment was made to monitoring the effects of the manipulation.

Components of the process

Objectives and indicators for habitat management

Each habitat management issue will have its own set of specific objectives. Most specific objectives, however, derive from one of four general goals for ecosystem management: (1) to maintain or increase (optimize) the harvest or yield of fish from an ecosystem; (2) to protect or conserve healthy ecosystems from the effects of human activities; (3) to preserve pristine or undisturbed natural systems; and (4) to restore degraded ecosystems to a healthier state.

The first of these goals reflects the traditional goal of fisheries management, namely the maintenance of productive fisheries in the face of pressures for alternative uses of the habitats upon which the fisheries depend for sustainable production. It is this goal that is most easily reflected in the concept of productive capacity as defined by DFO (1986), although the federal policy certainly recognizes the importance of the other goals. The remaining three goals reflect a more contemporary view of ecosystems as having value beyond simply their utilitarian purpose (e.g., Norton 1987; Callicott 1991; Olver et al. 1995). The second and third goals will generally apply to situations where a regulatory agency is evaluating potential effects of a proposed habitat manipulation, while the fourth is more concerned with determining the most suitable manipulations to achieve a particular restoration objective (type A issues). Sometimes, however, the distinction between these categories can break down, as is the case for the example presented above. If the dam is viewed as a man-made structure that has "degraded" access to the headwaters for migratory fishes the goals and objectives will be different than if the headwater areas are viewed as relatively healthy ecosystems at risk of invasion by non-native migratory species.

The most suitable set of indicators for a particular issue will depend upon the nature of the issue and the management objectives. Traditionally, the most commonly used indicators have been population-level measures of either supply (standing stock, production) or use (yield, catch rates). When the objectives include community-level concerns, measures of community status such as species diversity, species richness, and genetic diversity may provide more suitable indicators. Issues involving sub-lethal effects may call for other indicators such as contaminant levels, physiological changes, or behavioral changes. Finally, there are often practical impediments to the use of population- or community-level indicators. Sometimes, these indicators are simply too costly to accurately measure; alternatively, they may not be sufficiently diagnostic

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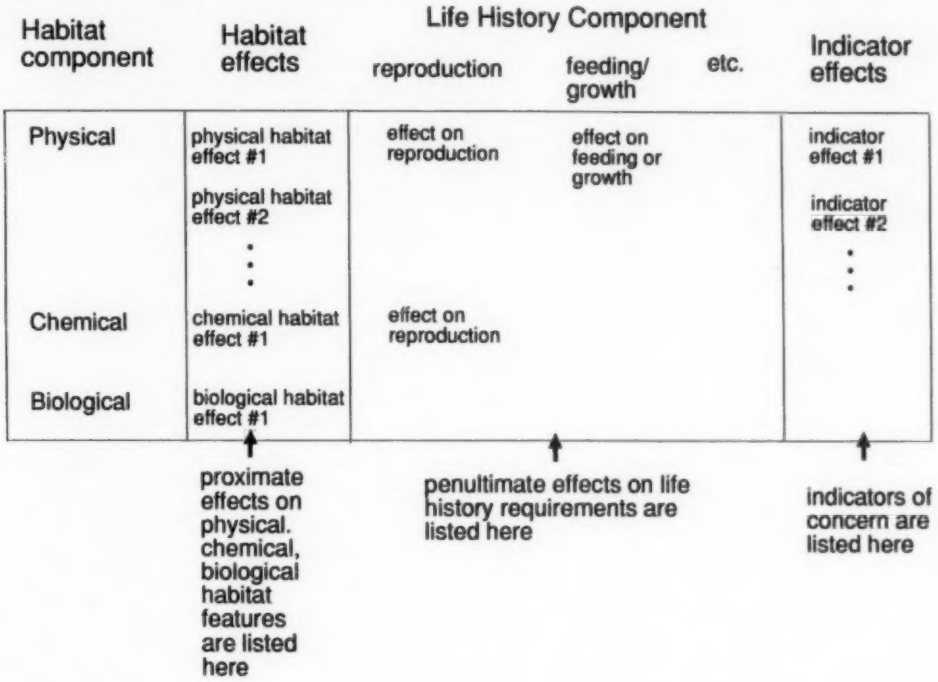
Fig. 1. A general matrix to summarize the possible linkages between habitat modifications and ecological indicators. The matrix details the hypothesized changes to physical, chemical, and biological components of habitat and their potential effects on species life-history requirements and, ultimately, on population- or community-level indicators.



of the habitat changes that are being evaluated. In such cases, surrogate, nonbiological indicators (e.g., physical or chemical changes) may be proposed, although the utility of these measures as indicators depends crucially on a previously demonstrated linkage between the surrogate indicator and the ecological effect it is intended to reflect. The process described below provides an objective approach for determining whether the use of a surrogate indicator is defensible.

Cause–effect pathways

The first steps of the process define the scope of the problem, setting the context for the analysis that follows. The type of issue (A or B) is determined together with the set of habitat manipulations under consideration. The issue is placed in the context of management goals and more specific objectives for the system(s) that stand to be affected, and indicators are identified that will provide measures of whether objectives are being met. Now a systematic process must be followed to evaluate the range of effects that the manipulations might be expected to have on the chosen set of indicators. While it is relatively easy to speculate on the range of possible effects of a particular manipulation, determining which of these possible effects are likely to occur in the specific instance under investigation is more challenging and calls for a rigorous, comprehensive approach that not only identifies likely effects but also exposes critical uncertainties.

Virtually without exception, the linkages between habitat changes and ecological effects involve a complex network of cause and effect. Rarely is only a single pathway involved, so the relative importance of different pathways must be assessed, not to mention possible interactions. Each cause–effect pathway typically involves several steps. Removing a dam can involve alterations to hydrology, sediment dynamics, thermal regimes, and species composition above and below the former dam site. Each of these proximate effects may translate into a variety of further effects such as patterns of seasonal floodplain inundation, bank erosion, changes to stream channel morphology, and contaminant exposure for top predators. These changes in turn can affect the ability of species to fulfil their life-history requirements. Finally, these penultimate effects on life history may translate into changes to the chosen indicators of ecological effect.

We propose a two-stage approach to describing and evaluating this potentially complex network of habitat change → ecological effect linkages. The first stage is to divide the proximate effects of habitat changes into physical, chemical, and biological components; to divide the possible penultimate effects on the indicator organisms into broad life-history categories; and to summarize this information in a matrix (Fig. 1). The second stage involves recasting the cause–effect linkages implied by the matrix into a series of multistage hypotheses that can be systematically evaluated for evidence to support (or refute) the hypothesized cause–effect pathway. The process is designed to allow the practitioner to judge the likelihood of desirable effects and, equally important, the uncertainty associated with this judgement. A similar approach has been used

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Table 1. Habitat change → ecological effect matrices for a migratory brook trout population.

Habitat component	Habitat effects	Life-history component: Reproduction	Feeding/growth	Cover/survival	Migration	Indicator effect
		Access road construction				
Physical	Creation of physical barriers to movement				↓Access to spawning and rearing areas	↓Production
	Acute exposure to sediment inputs	↑Egg mortality	↓Food consumption	↓Juvenile survival		↓Abundance
	Direct destruction of spawning and nursery habitat	↑Egg mortality		↓Juvenile survival		↓Genetic diversity
		Logging				
Physical	Changes to watershed hydrology	↓Incubation success		↓Overwinter survival		↓Production
	↑Sediment inputs	↑Egg mortality	↓Food availability			↓Abundance
	↓Streamside shading		↑Food availability	↓Survival during temperature extremes		↓Genetic diversity
Chemical	↑Nutrient inputs		↑Food availability			

successfully in an environmental assessment context (Bernard et al. 1993).

The best way to explain and demonstrate the generality of this process is to illustrate it using realistic and contrasting examples. We will use four habitat alteration examples, two for a migratory salmonid species and the other two for a littoral centrarchid community. These examples are not intended to be comprehensive treatments. Rather the examples are provided to illustrate the process we propose and to expose some of the challenges associated with its use.

The habitat change → ecological effect matrix

Example 1. Timber management and migratory brook trout (Salvelinus fontinalis) populations

Historical accounts suggest that large, migratory brook trout populations, locally known as "coasters," were once an important part of the Lake Superior fishery (Roosevelt 1865; Shiras 1927). The coasters utilized Lake Superior tributaries for spawning and early rearing, and then moved to the lake where they grew to adult sizes in excess of 2–3 kg. As a result of exploitation and, perhaps, habitat loss, today only remnant populations remain in localized, relatively remote areas (e.g., Isle Royale, Nipigon River). Protection of these remnant stocks and restoration of stocks into streams where they historically occurred have become management priorities for fisheries management agencies around Lake Superior. An important component of this effort is to ensure that aquatic habitats in areas where coasters presently exist or in areas where restoration is targeted remain in a state that allow coasters to complete their riverine life-history requirements. The management objective in this case is to protect habitats in areas currently or potentially utilized by coaster brook trout from the effects of human activities. For streams currently utilized by coasters, an appropriate indicator might be the maintenance of juvenile (presmolt, age 1 and older) brook trout summer densities within the range of one to five fish per 100 m^2 of available habitat.

Much of the Lake Superior watershed is forested and is the object of an economically important timber industry. Both access road construction and clear cutting can have effects on aquatic habitats. The former results in a relatively localized, direct habitat alteration, while the effects of the latter are thought to occur on a larger scale and include indirect influences. Both activities, combined with the objective stated above, constitute examples of type B issues, in which the purpose is to evaluate the potential effect of a human activity on aquatic habitat.

Access road construction could affect coaster brook trout habitat in several ways (Table 1). If stream crossings result in excavation or burial of substrate typical of quality brook trout spawning habitat, localized, but permanent habitat loss may occur. During construction of both roads and crossings, the opportunity for large increases in sediment loads to streams arises. Such inputs of sediments will likely increase stream turbidity and alter substrate composition. Increased suspended sediment concentrations in streams can also affect instream erosion by altering flow characteristics and frictional forces within the channel (Parker et al. 1982; Gordon et al. 1992). These effects are likely to be distributed over a wider area of aquatic habitat but are also likely to be transient in nature. Depending on the design and construction of the crossings, access of brook trout to upstream spawning areas (or overwintering habitats) may be restricted. This is an example of a local alteration having a potentially wide ranging effect. Together these examples illustrate how consideration of spatial and temporal scales is a critical component of the evaluation of habitat effects.

Clear-cutting can also affect coaster brook trout habitats through a variety of pathways (Table 1). Removal of a large fraction of the forest cover from a catchment may have significant effects on the basin's hydrology, including groundwater

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Table 2. Habitat change → ecological effect matrices for a nearshore centrarchid community.

Habitat component	Habitat effects	Life-history component: Reproduction	Feeding/growth	Cover/survival	Migration	Indicator effect
		Macrophyte addition				
Physical	↑Macrophyte density	↑Spawning success		↓Predation risk		↑Community production
	↓Fetch					
	↓Erosion and siltation	↓Egg mortality				↑Species diversity
Chemical	↓Turbidity		↑Food availability	↑Predation risk		
Biological	↑Detritus		↑Food production			
		Urbanization				
Physical	↑Sediment loads to nearshore	↓Spawning success	↓Food availability	↓Predation risk		↓Community production
	↑Temperature	↓Egg mortality				↓Species diversity
Chemical	↑Nutrient inputs		↑Food availability			
	↓Oxygen levels	↑Egg mortality		↑Juvenile mortality		
	↑Contaminant loadings	↓Reproductive success				↑Body burdens

dynamics and overall basin water yield. Nutrient budgets may also be affected. During both the tree removal operations and the early period of subsequent regeneration, sediment dynamics can be greatly altered, especially if cutting is permitted in the riparian zone. Finally, removal of riparian vegetation may also expose stream reaches to increased solar radiation and thus increased water temperatures.

The habitat alterations described above could have a variety of effects on coaster brook trout populations. Removal or burial of spawning habitat, accumulation of fine material in spawning gravel, or reduced access to spawning areas will all affect spawning success. Reduced groundwater discharge may also render traditional spawning habitats less suitable. High sediment loads may affect juvenile feeding success. Increased nutrient loads together with increased temperatures and solar radiation due to reduced shading could lead to increased growth and survival, provided levels do not become excessive. As well, changes to groundwater inputs and reduced shading will interact to affect temperature extremes in summer and winter and through this, juvenile brook trout growth and survival.

Example 2. Littoral centrarchid communities in Great Lakes coastal wetlands

Often, interest in the effects of habitat change is directed towards the community, rather than the population level. One example would be the complex of warmwater species, often dominated by centrarchids, found in nearshore embayments and wetlands around the Great Lakes. The vast majority of shoreline wetland areas around the Great Lakes have been lost during the past 100 yr as a consequence of the settlement and industrialization of the basin. Accordingly, much recent concern has been expressed about the protection and restoration of the few remaining areas. Two relevant but contrasting habitat management issues for Great Lakes littoral centrarchid communities are (1) will creation (addition) of areas of macrophytes benefit this fish community; and (2) will urbanization of lands adjacent to and draining into nearshore habitats degrade this community. The first of these is a type A issue, and is frequently found as a proposed strategy in RAPs. The second is a type B issue. The two issues also differ with respect to scale, the former operating primarily at the local, within-wetland scale while the latter embraces a larger, watershed scale that includes the littoral zone and the (urbanizing) upland areas that drain to the wetland. For both issues, the (ecological) management objective could be stated as to restore (issue 1) or maintain (issue 2) the health and productive capacity of the warmwater fish community in the affected nearshore areas. Indicators of the achievement of this objective would include (1) restoring or maintaining the abundance and production of species at levels within the natural bounds of variation found at healthy sites; (2) maintaining or increasing species diversity; and (3) maintaining levels of contaminants in fish low enough to allow safe human consumption.

The habitat change → ecological effect matrices for these examples have the same structure as for the migratory brook trout example (Table 2). Habitat changes caused by the addition of macrophytes would include the obvious consequence of increased macrophyte density (at the site level), but also indirect effects such as increased detritus production, and potentially reduced fetch, erosion, and turbidity. Habitat changes resulting from watershed urbanization are more difficult to predict and measure; in general effects on fish habitat in nearshore areas will result from changes in the quantitative and qualitative characteristics of streams draining from the urbanized area into the nearshore habitats. Urbanization tends to increase the imperviousness of watersheds, leading to changes in discharge patterns. Streams experience higher peak flows and lower base flows (Klein 1979). The hydrological changes and the increased erosion that tends to follow can result in greater sediment and nutrient inputs into nearshore areas. Reductions in oxygen concentrations can result if nutrient inputs are excessive. Water temperatures and contaminant levels may also be elevated.

These changes could lead to several effects on centrarchid communities utilizing these nearshore habitats. Increased macrophyte cover (Table 2) may provide cover and spawning habitat for fish and may increase food production resulting

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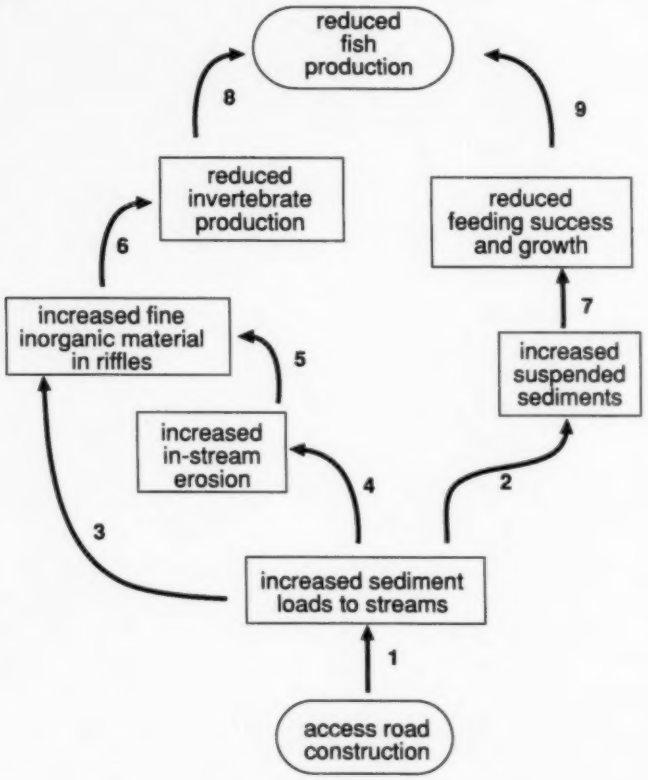
Fig. 2. An example hypothesis-of-effect from the coaster brook trout – forestry access road case. The habitat manipulation is listed at the bottom and the various intermediate effects are depicted as boxes connecting the habitat change to the indicator listed at the top. The numbered arrows connecting each box represent the individual steps (sub-hypotheses) in the cause–effect pathway(s) leading from the habitat manipulation to the indicator.



from elevated primary production and especially detritus. Reductions in fetch, erosion, and turbidity may enhance feeding success or survival of incubating eggs but may also increase vulnerability to visual predators. As well, reduced turbidity may further enhance primary production, thereby allowing additional expansion of macrophyte cover in the affected areas.

Habitat changes potentially resulting from watershed urbanization can affect reproduction, feeding, and cover for fish (Table 2). Sediment loading may have a negative effect, specifically on the quality of spawning habitat for fishes, and on the habitat of the biota in general. Loadings of fine sediments will also increase turbidity, thereby reducing visibility for visual predators, as well as light penetration and, consequently, macrophyte growth. Increases in nutrients may increase both primary and secondary production, but changes in species composition may also occur. If nutrient inputs are excessive, lower oxygen levels may result because of decomposition and excessive biological oxygen demand. Another potential impact of watershed development is an increase in anthropogenic contaminants (e.g., lead and cadmium from automobiles, organochlorines from various sources). Contaminants may affect the edibility of fish and may also have short- or long-term effects on life-history processes such as reproduction or survival rates.

Hypotheses-of-effect: evaluating knowledge and uncertainty

The matrices presented in Tables 1 and 2 provide summaries of the possible effects of concern for a particular issue. Each matrix is a conceptual model of the connections between a habitat manipulation and the potentially affected ecosystem. Once a matrix has been developed, a systematic process of evaluating relevant knowledge can begin. The elements of the matrix imply a network of cause–effect linkages that connect the habitat changes to ecological effect indicators. Individual cause–effect pathways can be extracted from the matrix that form a multiple-step hypothesis that connects the initial habitat manipulation to the ultimate effect. We refer to these pathways as "hypotheses-of-effect."

Each step or linkage in an overall hypothesis-of-effect should be described as a statement that constitutes, in effect, a potentially testable (sub-)hypothesis. For example, the first linkage in an hypothesis-of-effect connecting access road construction to coaster brook trout production via sediment load-

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ing impacts (Fig. 2) could read, "Forestry access road construction will lead to increased sediment loads to streams." Similar statements would be developed for each of the other linkages (2–9) depicted in Fig. 2.

The process of evaluating evidence then involves addressing a series of specific questions concerning each of the linkages in the overall hypothesis-of-effect: (1) How strong is the evidence supporting this linkage? (2) At what scale is it appropriate to evaluate or measure this linkage? (3) Are there other factors that, depending on their state, may affect the significance of this linkage? (4) What critical uncertainties exist that make it difficult to reach a firm conclusion on the likelihood of this linkage being true? (5) Assuming there is evidence for an overall effect on the indicator, can the effect be mitigated at the stage represented by this linkage?

Again, using the example of linkage 1 in the hypothesis-of-effect depicted in Fig. 2, the analysis might proceed as follows.

There is little doubt that, in the absence of any mitigative measures, the construction of forestry access roads will lead to increases in the loadings of suspended inorganic matter to streams, especially in the vicinity of stream crossings (Anderson 1971; Plamondon et al. 1982, cited in McNamee et al. 1988). The effect is likely to be greatest immediately downstream of crossings, diminishing as the suspended material is either diluted by mixing with water from other tributaries or deposited in low energy habitats such as pools. Forestry operations typically call for several crossings, sometimes of the same stream, however, so cumulative, larger scale effects cannot be ignored. The magnitude of this effect will depend on the topography and physiography of the areas, with the greatest concerns arising in areas with highly erodible soils and high relief.

In the rugged terrain north of Lake Superior where coaster brook trout are or were present, it is likely that significant sediment inputs would occur in the absence of mitigative measures. There are numerous techniques to mitigate increased sedimentation, however, such as silt curtains, coffer dams, and retention ponds (OMNR 1990; Kerr 1995). Provided these measures are satisfactorily applied, the increased inputs of sediments during and after construction can be minimized to the point where inputs are modest and the effects, if any, are very localized.

In this example, the linkage is relatively well understood as are the opportunities for mitigation. A fully developed analysis of this linkage should provide more detail (or a summary of useful references) on the circumstances wherein concerns are likely to be the greatest (e.g., types of road or crossing construction, critical soil characteristics) and on prescriptions for mitigative measures. In other cases, the evidence for the linkage being true may be much less clear. For example, linkage 8 in the brook trout hypothesis (Fig. 2) might read, "Reductions in invertebrate production from riffles will lead to reductions in juvenile brook trout production." Although it is well known that stream-dwelling juvenile salmonids depend on drifting invertebrates as their primary food source, defining quantitative relationships between secondary production and fish production has proven difficult (Hynes 1970; Richardson 1993; Waters 1993). Thus, while it is virtually certain that drastic reductions in invertebrate production will affect trout production, it is more difficult to predict the consequences of subtle changes (e.g., a 20% reduction persisting for one growing season). Evaluation of linkages such as this should include an attempt to bound the magnitude of effect that is likely to be detectable.

When the issue involves habitat modification effects on entire communities, particularly indirect effects such as urbanization effects on aquatic communities, the uncertainty surrounding individual linkages can become critical. One of the hypotheses-of-effect in the littoral centrarchid community example concerns effects of urbanization on centrarchid fishes as mediated through a sedimentation – loss of macrophyte production pathway. The series of pathways and linkages leading from urban development in a watershed to effects at the fish community level in nearshore habitats are numerous (Fig. 3). Some of the linkages are supported by strong evidence, but others are not. Confounding factors often apply at a specific effect level, and a particular cause–effect linkage is sometimes difficult to test. For example, linkage 4 in Fig. 3 could be defined as, "Increased instream erosion causes increased turbidity in receiving embayments." At Cootes Paradise in Lake Ontario, and Rondeau Bay in Lake Erie, high turbidity was linked at least in part to input of suspended solids from receiving tributaries (Hanna Associates Inc. 1984; Painter et al. 1989, 1991). However, turbidity was also attributed to the effect of wind, and in the case of Cootes Paradise, to increased algal primary production caused by elevated nutrient inputs and to the activity of carp (*Cyprinus carpio*). For this linkage, many cofactors would have to be investigated before links between the stream water quality and water turbidity of the receiving embayment could be isolated.

The spatial and temporal scales which apply also complicate this linkage. Cause and effect are spatially separated (upstream urban construction – downstream wetland turbidity), leaving room for proximate confounding factors to influence turbidity (wind, carp) as well as the distal factor of immediate concern (urbanization, suspended solids in the stream). Resuspension of materials in the embayment by wind-generated currents, contributing to turbidity, will increase with time as more material moves downstream and accumulates. Appropriate mitigation to reduce existing turbidity or to prevent future problems must address all significant contributing factors. Mitigation that focuses on preventing soil erosion and the resulting increases in inorganic suspended solids in stream effluent may help reduce turbidity, but increased nutrient loads and concurrent increases in stream temperature from urban development could override these mitigations. Ultimately, effective mitigation will require that the extent of urban development that is allowed in any one watershed be limited (Klein 1979), and that the mitigation actions be broad and multifaceted (e.g., Marshall Macklin Monaghan Ltd. 1994).

Higher in the pathway leading to community fish production (Fig. 3), other uncertainties become apparent. In the centrarchid example, species richness is assumed to be the fish community indicator of interest and is the accepted measure of productive capacity. Several investigators have demonstrated a positive link between macrophyte abundance and fish species richness in inland lakes (Keast et al. 1978; Bryan and Scarnecchia 1992), lower reaches of rivers (Killgore et al. 1993), and in the Great Lakes (Randall et al. 1995). Macrophyte reduction, resulting from increased turbidity, would thus be of concern. However, several factors associated with

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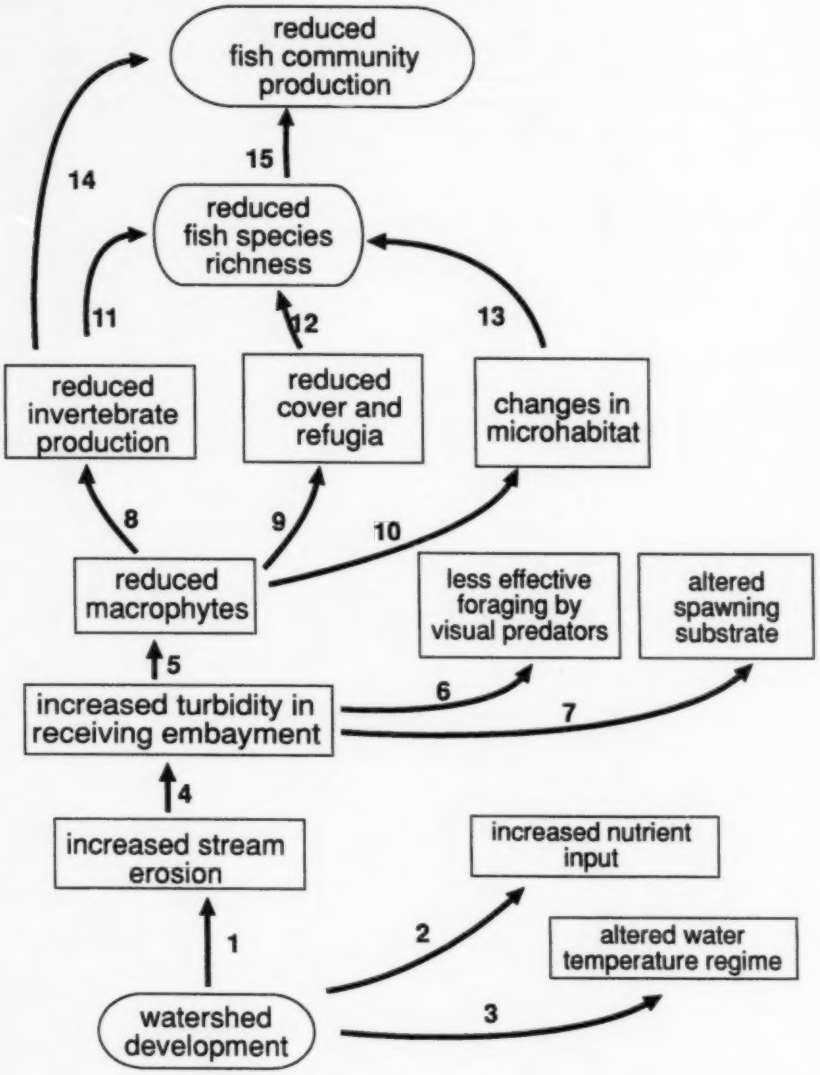
Fig. 3. An example hypothesis-of-effect from the littoral centrarchid – urbanization case. The cause–effect pathway, which begins with "increased instream erosion," is one of several possible hypotheses-of-effect relevant to this case. The first step in two other pathways (nutrient loadings, temperature changes) are also presented. Each pathway would require a separate analysis, including consideration of interactions among pathways where appropriate.



macrophytes may account for the increase in species richness. Macrophyte beds are used by fishes for several functions: phytophilic species (Balon 1975) use macrophytes as spawning substrate or as refugia for reproduction; macrophyte beds provide a rich feeding environment (Killgore et al. 1993); and macrophytes provide cover and refugia from predators (Rozas and Odum 1988). To understand cause and effect between macrophyte abundance and a fish community indicator like species richness, at least three linkages must be considered (Fig. 3, linkages 11, 12, and 13). Similarly, mitigation must consider all factors associated with macrophytes (primary and secondary production, refugia and structure, and unique microhabitats); focusing on only one aspect (say using artificial habitat structure to replace the lost cover) would not result in compensation.

Uncertainties about species interactions and species-specific reactions to changes in habitat may further complicate these considerations. Because of unpredictable predator–prey interactions, and the role of cover, the response of individual species to macrophyte removal may not be fully understood. For the centrarchid largemouth bass (*Micropterus salmoides*), Durocher et al. (1984) reported a linear positive relationship

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between macrophyte cover and recruitment to harvestable size. In contrast, Bettoli et al. (1992) found that the elimination of vegetation had a positive effect on bass populations, because the lack of cover allowed the bass to become piscivores at a smaller size and thus significantly increase their growth rate during their first year. The structure of the forage fish community shifted, but ample fish prey existed for the largemouth bass before and after vegetation removal. The linkages between habitat and fish, when considered at the community level, will sometimes be poorly understood or unpredictable, even for well-studied species.

Enough evidence exists to indicate that macrophyte reduction, caused by increases in turbidity, will result in a decrease in fish species diversity. The pathways leading to this change are diverse and sometimes poorly understood, however. The matrix approach and a consideration of the hypotheses-of-effect linkages illustrate the complexity of the effects of habitat alteration at the community level and the number of issues that managers must face when trying to mitigate for the potential loss of habitat quality.

The final step in the process is to reach an overall conclusion regarding the hypothesis-of-effect. This conclusion should state whether an undesirable effect is likely to result from this cause–effect pathway. It should summarize the circumstances under which such an effect might be expected and should recommend ways to mitigate the effects if necessary. Often there will emerge a range of options for mitigation of the effects, ranging from costly interventions with a high likelihood of preventing the negative ecological effects to less expensive actions with greater uncertainty as to their effectiveness. These options should be summarized as part of the conclusions, together with an assessment of the risks and benefits associated with each.

In the majority of instances, the uncertainties will be sufficient to warrant research and monitoring recommendations as well. These recommendations should include details on what should be measured, as well as the spatial and temporal scales of observation. Monitoring provides opportunities for reducing uncertainties for the future; these opportunities should be considered when developing a recommendation.

Conclusions and recommendations

The matrix approach combined with the hypothesis evaluation method provides a systematic procedure for evaluating the effects of habitat change on ecological indicators of interest to resource and environmental managers. The method makes explicit the cause–effect linkages that must be considered if one is to rigorously evaluate the potential impacts of a habitat manipulation. Further, it provides an mechanism for considering related issues, such as that of scale and of the confounding effects of other forces on the linkage between habitat changes and ecological effects.

The specification of the matrix and evaluation of the evidence using the hypotheses-of-effect for a particular habitat management issue constitutes a substantial task. Reviewing the literature alone (much of which is not found in primary, peer-reviewed sources) will require a significant effort. It is unrealistic to expect that this level of effort can be directed at each issue confronted by the biologist asked to determine the appropriate action (i.e., do not allow habitat modification, compensate, more research or information required, etc.). On the other hand, there is redundancy in the habitat management issues faced by biologists throughout North America. To be useful, the framework we describe above should be applied to classes of habitat manipulations (e.g., road crossings, macrophyte plantings) and the matrices and hypotheses developed so as to be applicable over a broad geographic range. To achieve this generality the analysis of linkages within the hypotheses of effect will have to include consideration of how such contextual elements as physiography, topography, and climate affect the significance and magnitude of the linkage. If the analysis is done in this way, the results can then be applied to any specific issue that falls within that class, without redevelopment of the entire framework. We would challenge regulatory agencies to take the initiative to apply this framework, ideally in collaboration with proponents responsible for the relevant manipulations (e.g., forest industry for access roads).

For any habitat manipulation to which this framework might be applied, one of the inevitable outcomes will be the exposure of the uncertainty concerning some, if not all, of the linkages in the hypotheses-of-effect. This must not be viewed as a weakness of the framework. On the contrary habitat management processes that do not probe the cause–effect linkages to the extent done by this framework will tend to overlook some of the uncertainties, with (at least) two negative consequences. First, manipulations may be allowed for which the "best guess" would suggest there is no likely detrimental effect on the indicator of interest, but for which there is a substantial hidden risk. Conversely, conservative decisions may be made regarding a manipulation because the highly uncertain best guess suggests a detrimental impact. Second, ignoring key uncertainties squanders opportunities to learn and thereby reduce uncertainties for future decisions concerning the same issue. Identification of uncertainties exposes opportunities for adaptive management (Holling 1978; Walters 1986). Habitat management issues frequently offer opportunities for application of adaptive management principles, because similar manipulations are repeated in space and time, thereby affording the opportunity for experimental design and replication of adaptive experiments.

Another use of this framework for habitat management lies in the determination of suitable surrogate indicators of ecological effects. Generally, the ecosystem components or attributes that constitute the endpoints of our cause–effect pathways linkage tend to be population- or community-level attributes that can be costly and difficult to measure. To justify using a surrogate measure (e.g., water-quality parameters, fish growth) as the indicator, it is important to demonstrate an unequivocal linkage between the surrogate and the indicator of interest. Evaluation of the linkages in the hypotheses-of-effect that connect habitat or life-history attributes with population or community indicators should include whether the former provide reliable surrogates for the latter. Because effects monitoring should be a key component of habitat management (especially adaptive habitat management), and because monitoring fish population and community status can be both costly and burdened with measurement problems, the development of reliable surrogate measurements is a priority.

The future success of habitat management demands that we have mechanisms for examining and making the best possible use of what we know about linkages between habitat manipulations and ecological effects. Not only should we be making

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the best possible decisions regarding habitat manipulations, but we should also exploit opportunities for increasing our knowledge in areas where uncertainty makes it difficult to predict effects. The concept of productive capacity and the Canadian habitat policy that utilizes this expression have forced us to look more carefully at our knowledge of linkages between habitat change and ecological effects. The framework described in this paper offers a systematic methodology for organizing this knowledge. Whether this methodology is adopted or not, our most important recommendation is that, if we are to advance beyond the piecemeal one issue at a time approach to habitat management that is the current norm, an approach such as the one described herein will have to lead the way.

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A commentary on the role of institutional arrangements in the protection and restoration of habitat in the Great Lakes

Joseph F. Koonce, Vic Cairns, Al Christie, Douglas P. Dodge, Andy Hamilton, Henry Lickers, Brian McHattie, Don Roseboom, and Charlie Wooley

Abstract: The common features of institutional arrangements associated with successful restoration and protection projects within the Great Lakes basin were extensive partnerships and involvement of local interests. We found that separation of water quality, water quantity, and resource management authority often gave rise to conflicting management actions and that the fundamental lack of coordination among national, state or provincial, and local government programs contributes to failed institutional arrangements. Even successful projects require dedicated individuals to find ways of making existing institutional arrangements work. We find that attempts to reorganize government agencies may be less effective than an approach to empowering local interests to plan and implement better habitat management projects. Our basic recommendation is to have governments empower and support communities to take responsibility for the natural environment.

Résumé : Les mesures institutionnelles qui se sont traduites par le succès des projets de restauration et de protection dans le bassin des Grands Lacs étaient caractérisées par d'importants partenariats et par la participation d'intervenants locaux. Nous avons constaté que, du fait que la qualité de l'eau, les volumes d'eau et la gestion des ressources relèvent d'autorités différentes, les mesures de gestion étaient souvent en conflit les unes avec les autres, et que le manque fondamental de coordination entre les programmes des gouvernements fédéraux, des États ou provinces et des administrations locales était en partie responsable de l'inefficacité des mesures institutionnelles. De plus, quand un programme est couronné de succès, il a fallu pour cela que des personnes dévouées trouvent des façons d'assurer le bon fonctionnement des mesures institutionnelles. Nous constatons que les tentatives de réorganisation des organismes gouvernementaux peuvent être moins efficaces qu'une approche visant à habiliter les intervenants locaux à planifier et à mettre en oeuvre de meilleurs projets de gestion des habitats. Nous recommandons principalement que les différents gouvernements habilitent les communautés et les aident à prendre en main leurs responsabilités en matière d'environnement.
[Traduit par la Rédaction]

Introduction

Habitat protection and restoration in the Great Lakes has more failures than successes. Despite commitments of the governments of Canada and the United States to "restore and maintain the chemical, physical, and biological integrity of the waters of the Great Lakes Basin Ecosystem" in the 1978 Great Lakes Water Quality Agreement, the state of habitat in the Great Lakes basin continues eroding (Dodge and Kavetsky 1994). Ultimately, habitat protection and restoration requires implementation of plans to manage habitat on an area basis. Fundamental disagreements and uncertainties about foundations for classification and inventory of habitat certainly impedes formulation of such plans, but we believe that fragmentation of authority for habitat management among various jurisdictions at several levels of government (federal, state or provincial, and local) creates more fundamental barriers. The purpose of this paper is to report the findings and conclusions of a review of the contribution of institutional arrangements to lagging habitat restoration and protection in the Great Lakes basin.

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Table 1. Summary of international agreements and laws of Canada and the United States that are relevant to the protection and restoration of habitat (after Dodge and Kavetsky 1994).

Authority (and decade)	Legal citation (if known)	Species or target habitat
International/Binational		
North American Waterfowl Management Plan (1980s)		Conservation of waterfowl habitat
Migratory Bird Convention (1910s)		Migratory birds
Great Lakes Water Quality Agreement (1970s)		Wetland preservation
Strategic Plan for Great Lakes Fisheries Management (1980s)		Binational management for fish species and their habitats
RAMSAR Convention on Wetlands of International Importance (1970s)		Important wetlands identified and protected through legislation
United States		
Fish and Wildlife Coordination Act (1930s)	16 USC 661–667e	Fish and wildlife, must be a federal project
Great Lakes Fisheries Act (1950s)	16 USC 931–939c	Fish habitat, sea lamprey control
Endangered Species Act (1970s)	16 USC 1531–1543	Any listed or candidate species habitat
Migratory Bird Treaty Act and Migratory Bird Conservation Act (1910s)	16 USC 701–718i	Migratory birds
Emergency Wetlands Resources Act (1980s)	P.L. 99–645	Wetlands
Anadromous Fish Conservation Act (1960s)	16 USC 757a–757g; 79 Stat. 1125	Anadromous fishery resources
Federal Power Act (1920s)	16 USC 791a–825r; 41 Stat. 1063	Fish and wildlife resources
Sikes Act (1960s)	USC 670a–670o; 74 Stat. 1052	Fish and wildlife, especially military and tribal lands
North American Wetlands Conservation Act of 1989	16 USC 4401–4412	Wetland ecosystems and other habitats for migratory birds and other fish and wildlife
Canada		
Migratory Bird Convention Act		Protects migratory birds and habitat
Canada Wildlife Act		
Federal Policy of Wetland Conservation		
Federal Fisheries Act		Protects fish habitat

Evolution of government policy on habitat

Origin of law

Following widespread deforestation and land clearing for agriculture, several significant federal habitat policy developments occurred in the middle to late 1800s: the Swamp Acts of 1850, implementation of policies to protect Great Lakes shipping, and the drive for improved access to the developing metropolitan areas (Edsall et al. 1988). The Swamp Acts encouraged the draining and diking of "worthless public lands, lying as marshes along adjacent water courses" (Donaldson 1970). Continued drainage of low lands for agriculture along connecting channels and other areas within the Great Lakes system was followed by urban sprawl and industrial development, which required bulkheading and seawall construction along the shoreline. Constructing canals, followed by deepening and maintaining navigation channels has continued unabated over the last 140 yr and dredge material prior to 1970 was usually disposed of in open, adjacent waters (Larson 1981).

Against this backdrop of public policies to convert and degrade habitat, federal policies emerged in both Canada and the United States to protect specific species and (or) their habitats based on the Public Trust Doctrine concepts of law. Public Trust Doctrine concepts have persisted in European, English, and American law throughout history, with roots in Greek and Roman times. The Institutes of Justinian in the sixth century A.D. stated "by the law of nature these things are common to mankind—the air, running water, the sea and consequently the shores of the sea." Bean (1977) noted that, beginning with a U.S. Supreme Court ruling in 1842, wildlife is held in trust for all citizens. Bean (1977) further points out,

> "With new federal laws came requirements limiting the taking of wildlife, regulating wildlife trade and commerce and providing for the acquisition and management of wildlife habitat. Today over 100 treaties, international agreements, federal statutes, executive orders and federal regulations provide a complex array of interrelated and sometimes overlapping requirements. Aside from a useful reprinting of federal wildlife statutes and a few legal articles, no report describes and analyzes how all of these federal laws have evolved and how they interact with each other. Moreover, the responsibility for interpreting and enforcing these many separate and diverse laws is fragmented among many public agencies. As a result, it is difficult, if not impossible, to fashion and implement a comprehensive and consistent national program for the protection and conservation of wildlife."

Laws and agreements

Table 1 summarizes the review of Dodge and Kavetsky (1994) of the laws related to habitat in Canada and the United States.

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Although Table 1 is by no means comprehensive, much of the habitat specific law is recent. Another clear trend from Table 1 is that, historically, the U.S. federal emphasis has been on species such as migratory birds and anadromous fish, which had utility to humans. Vaughan (1994) observed that,

> "Congress and subsequently the various state legislatures, have taken a route of generally dealing with one environmental problem at a time; there simply are no laws that try to deal with the wide range of interrelated problems in a holistic fashion."

His advice when dealing with an environmental problem was to look at the statute that most fits the problem and then determine if other laws also apply. Criminal sanctions, available in many of these laws, received very little use.

The ongoing loss and impairment of habitat indicate that the U.S. federal government's policies have not yet been successful in reversing the trend of the last two centuries. Whether or not the policies have slowed the rate of change cannot be ascertained because the data are not available or are inadequate to accurately determine basin-wide trends. Within the United States, wetlands are managed through a mixture of federal, state, and local initiatives, with public input from citizens and interest groups. The federal government's primary tool for protecting wetlands is Section 404 of the Clean Water Act. In accordance with Section 404, the U.S. Army Corps of Engineers (Corps) and the Environmental Protection Agency (EPA) regulate the discharge of dredged or fill materials in "all waters of the United States." Under Section 404 the Corps considers the advice of EPA, the U.S. Fish and Wildlife Service (FWS), the National Marine Fisheries Service (NMFS), other agencies, and the public when deciding whether to issue or deny a permit. The State of Michigan has assumed administration of the Section 404 program. Most, but not all, wetland permit actions are handled by the Department of Natural Resources in Michigan. The other states in the basin also have wetland management laws that afford varying levels of protection to wetlands, but each state operates independently according to its own laws.

In Canada, habitat protection is a federal and provincial partnership. The Fisheries Act provides the basis for protection of aquatic habitat that meets the definition of fish habitat (Dodge and Kavetsky 1994). In Ontario, most of the habitat protection is driven by land-use planning under the Ontario Planning Act. This Act sets the process for evaluating development proposals and contains protection policies for wetlands. Ontario Ministry of Natural Resources (OMNR) is the provincial agency enforcing the Federal Fisheries Act and provides comment on development proposals. Municipal Affairs enforces the Planning Act and Ministry of Energy and Environment promulgate and enforce pollution regulations. At the regional level, Conservation Authorities establish flood and fill regulations for streams on a watershed basis. Increasingly, Conservation Authorities are becoming involved in habitat protection and rehabilitation (especially wetlands), subwatershed plans, working with landowners, and on behalf of OMNR, commenting on development proposals. Regional municipalities all have official plans, which outline planning policies including protection of local natural areas and itemize applicable Conservation Authority and provincial policies. Finally, local municipalities develop more detailed implementations of official regional plans but also must resolve conflicts in priorities of development and habitat protection.

Habitat interests of indigenous cultures

Under provisions of long-standing treaties and recently adjudicated agreements, U.S. Tribes have a mandate for management of treaty waters of the Great Lakes. Through the Chippewa–Ottawa Treaty Fishery Management Authority and the Great Lakes Indian Fish and Wildlife Commission, U.S. Tribes participate as management jurisdictions in the Joint Strategic Plan for Management of Great Lakes Fisheries (GLFC 1980). First Nations of Canada also have claims to resources of the Great Lakes, but rights and responsibilities of the First Nations are under active negotiation with both federal and provincial government agencies.

Governance and decision making of indigenous peoples for Great Lakes issues is fundamentally different from other governmental programs in Canada and the United States. Indigenous culture and the land are intrinsically connected through the Great Law, which underlies the spirituality of aboriginal peoples of North America. Rights to use the resources of the Great Lakes are thus bound to responsibilities of stewardship, but without the mantle of stewards. Guiding responsible use of the resources of the Great Lakes is Wisdom of the Elders as expressed in Traditional Environmental Knowledge (Martinez 1994). A consequence of this orientation to environment is that decisions about how to use the resources of the environment always involve deal making. Entering into deals means that there must exist an agreement to share some fundamental ways of balancing local desires with more global interests. For indigenous peoples, respect, equity, and empowerment are three central elements of deal making. In practice, therefore, "management" decisions of indigenous peoples often involve protracted negotiation and consensus seeking. Needless to say, this more holistic approach to decision making about environmental concerns does not fit well with more the formally structured legalistic and regulatory approach of other North American governance mechanisms. At the core, however, all institutional arrangements for governance are involved with reconciling the dichotomy of rights and responsibilities of local interests.

Analysis of the implementation of government policy

Structure of governmental arrangements in the Great Lakes as related to habitat issues

At the international level, Canada and the United States have developed several institutional arrangements to prevent disputes and to settle issues related to common Great Lakes resources. The primary vehicles for these arrangements has been a series of treaties and agreements (the last of which also involves Mexico): (1) Boundary Waters Treaty (BWT; 1909); (2) Migratory Bird Convention (MBC; 1916); (3) Convention on Great Lakes Fish (CGLF; 1955); (4) Great Lakes Water Quality Agreement (GLWQA; 1972, 1978, 1987); and (5) North American Waterfowl Agreement (NAWA; 1989).

Two trends are evident in these treaties and agreements.

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One trend is the increasing emphasis on ecosystem integrity, and the second is a trend towards increasing empowerment of regional and local decision making, which Francis et al. (1979) referred to as increasing federalism in the institutional arrangements of the Great Lakes Basin.

With these trends in binational agreements, Canada and the United States created formal organizations such as the International Joint Commission (IJC) and the Great Lakes Fishery Commission to serve these developing initiatives and created a context for the development of several informal governance mechanisms. One clear trend was the process of involving and then expanding the role of nongovernmental organizations (NGOs) and municipalities for habitat protection and restoration. The NGO (particularly Great Lakes United and The Nature Conservancy) involvement in the GLWQA, for example, began with observer status in the 1978 agreement and expanded to the role of participants in the shaping of the direction of the 1987 protocols. Similarly, the NAWA evolved from the MBC general agreements between Canada and the United States to a shared responsibility among NGOs (e.g., Ducks Unlimited and Wildlife Habitat Canada), the federal governments, and state and provincial governments. At the state and provincial level, habitat protection is accomplished jointly through the combined efforts of state and regional planning authorities. Funding often is provided or supplemented from city or county treasuries, and program delivery at the local level is accomplished through Soil and Water Conservation Districts, which are funded by state and municipal governments.

The formal binational agreements served as a catalyst and shaper of a number of important, but less formal and more ad hoc organizations. The Council of Great Lakes Governors provided a major stimulus for a Great Lakes Charter on Water Diversion from the basin. The Great Lakes Commission with funding from private foundations has taken the lead in developing a Great Lakes Ecosystem Charter. Great Lakes United has played an active role in building a public constituency for the Great Lakes. The International Association of Great Lakes Research provides a regular forum for addressing Great Lakes research and policy issues. Various regional, private foundations have been particularly effective in supporting integrated, third-party assessment of events in the Great Lakes Region. Foundations provided most of the support for a Royal Society of Canada – National Research Council joint assessment of progress under the GLWQA. Great Lakes Great Legacy was a similar initiative by the Institute for Research on Public Policy.

Case studies of interaction of habitat restoration or protection with institutional arrangements

Water quality agreement initiatives

The 1972 GLWQA was a response to the deteriorating condition of the lower Great Lakes. The setting of phosphorus loading targets for Lake Ontario and Lake Erie represented a major accomplishment to control eutrophication of these lower lakes (Vallentyne and Thomas 1978). Bertam (1993) reports evidence of the positive response of Lake Erie to these successful efforts to reverse the effects of cultural eutrophication. The 1972 and 1978 GLWQA were also concerned with reducing pollution of toxic substances in the Great Lakes, and the 1987 Protocols called for the creation of Lake-wide Management Plans (LaMPs) for pollutants to achieve the objective of virtual elimination of persistent toxic substances. Canada and the United States have been able to achieve dramatic reductions of critical contaminants (DeVault et al. 1994), but contaminants remain a long-term problem for the Great Lakes (Koonce 1994*a*).

Protection and restoration of habitat

U.S. federal arrangements

The 1972 Federal Water Pollution Control Act was passed by Congress to produce fishable and swimmable waters by 1983 and eliminate all pollutant discharges by 1985. The broad definition of pollutants included "dredged spoil" and caused concern for the Corps, the nation's largest navigational dredger. The Corps convinced Congress to give them the wetlands regulatory program but established an oversight and veto role (404(c)) for the EPA requiring them, in conjunction with the Corps, to promulgate guidelines governing the wetland permit program (404(b)(1) guidelines). The Act dramatically expanded federal jurisdiction from the Rivers and Harbors Act which defined jurisdiction as "navigable water" to "waters of the United States." The Corps narrow interpretation of the reach of section 404 brought a lawsuit from the National Resource Defense Council (NRDC) and the District Court for the District of Columbia ordered the Corps to revise its regulation to reflect the full regulatory mandate.

The EPA published the section 404(b)(1) guidelines in September 1975 to regulate the placement of "dredged or fill material" in waters of the United States. The 1977 Clean Water Act passed and reaffirmed coverage of "waters of the United States," ratified the Corps' practice of issuing general permits and authorizes the EPA to approve state programs (i.e., Michigan). It is also the first statutory mention of wetlands and explicit recognition of the FWS as a review agency. The Corps promulgated the revised regulations, which include a jurisdictionally expanded wetlands definition and adopt a version of the presumption against wetland filling in the EPA's 404(b)(1) guidelines. In 1980, the guidelines are revised and made stronger; the EPA declared guidelines are regulatory, not advisory, and are independent basis for prohibiting discharges, apart from the Corps public interest review.

Regulated activities under the 404 program typically include fill for development, water resource projects, infrastructure development, and wetland conversion for farming and forestry. The EPA and the Corps jointly administer the Section 404 program. The Corps responsibilities include day-to-day program administration, development of policy and guidance, and enforcement. The EPA's responsibilities include development and interpretation of the environmental criteria used in evaluating permit applications, determination of the scope of geographic jurisdiction, approval and oversight of state assumption of the program administrative responsibilities, identification of activities that are exempt (404(f)), review and comment on individual permit applications, authority to veto Corps' permit decision (404(c)), case specific elevation (404(q)), and enforcement. In addition, the FWS and the NMFS have important advisory roles in the permit process. The Fish and Wildlife Coordination Act and existing inter-

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agency Memoranda of Agreement require consultation and full consideration of the views and recommendations prior to the issuance of federal permits.

The federal agencies most responsible for wetland restoration are the FWS and the National Resource Conservation Service (NRCS) (formally known as the Soil Conservation Service). The FWS's program "Partners for Wildlife" restores wetlands on private lands through alliances between the FWS, other organizations, and individuals, while leaving the land in private ownership. The FWS restores, enhances, and manages wetlands in the North American Waterfowl Management Plan Joint Venture areas through partnerships with state agencies, public or private organizations, and private individuals. Other FWS efforts for protection include assisting U.S. Department of Agriculture (USDA) with implementation of the Swampbuster and Wetland Reserve sections of the 1990 Farm Bill by seeking new opportunities to protect wetlands using easements, leases, and the cooperation of private individuals.

The NRCS provides technical assistance to landowners for wetland restoration through various programs. These programs include general operations, the Conservation Reserve Program, the Stewardship Incentive Program, the Agriculture Conservation Program, and the Wetlands Reserve Program. The NRCS provides technical assistance to private landowners through Soil Conservation Districts.

The NRCS is responsible for providing technical assistance for programs that provide cost-share assistance (usually 25–50% of cost) for restoring wetlands with private landowners. These programs include the Conservation Reserve Program, Agriculture Conservation, and the Stewardship Incentive Program. This assistance includes investigating proposed sites, designing the needed practices, and overseeing construction. Recently, the NRCS received the administrative and technical authority for the Wetland Reserve Program. The Wetland Reserve Program provides private landowners the opportunity to restore wetlands and receive payment for either a 30-yr or permanent easement. This easement on the restored wetland assures that wetland values and functions will be maintained. In addition, the landowner receives a 50% cost-share assistance for construction costs to restore the wetland. Approximately $US 93 million was available in 1995 nationwide for the Wetland Reserve Program.

Ontario Drainage Act – Fishery Act conflicts

After the 1940s, farming practices and the demand for available land attracted agriculture to wetlands and other poorly drained soils as potential sites for intensive, row-crop farming (e.g., beans, corn, tobacco). To make this land usable, extensive tile and ditch drainage schemes were cofunded by farmers and the Ontario government. Many natural streams were severely altered to become drainage ditches, with subsequent losses of productivity and biodiversity of the native fish fauna and riparian vegetation. Although significantly altered by drainage activities, many of these former streams gradually reverted to productive units with meanders, instream structure, and riparian vegetation becoming reestablished naturally. Very quickly, however, drainage experts saw these changes as impediments to "good" drainage so that extensive "improvements" were undertaken to reset the system back to a straight, tetrahedral channel. Conflicts between drainage proponents and other resource managers were usually settled through mediation by drainage commissioners, who inevitably agreed that the loss of other amenities was acceptable in light of the gain to agricultural productivity. Ontario tended to use this avenue of mediation because all of the legal instruments were of provincial origin.

On the other hand, the Fisheries Act of Canada, the constitutional basis for fisheries and fish habitat management, specifically required that the Crown, e.g., the government of Ontario, was bound by the Fisheries Act. Therefore, any Ontario government agency was constrained, either in its own activities or those that it might fund, grant to, or support, to not intentionally destroy fish habitat, unless formal schemes to replace the lost habitat were approved by the federal Minister of Fisheries and Oceans.

To some, the obvious solution to the conflict were formal changes under the Fisheries Act to all and every exponent of schemes to redredge these partially recovered drainage ditches. However, the impasse and conflict was resolved through a required consultation system and through a code of practice that allows for drainage improvement, but saves many of the amenities associated with fish production and riparian vegetation.

Remedial Action Plans

Remedial Action Plans (RAPs) arose to address the problems of degraded environments in the Areas of Concern, which were identified sites within the Great Lakes basin. The 1987 Protocols of the GLWQA formalized commitment of the governments of Canada and the United States to promote a multistage planning and remediation process for each of the Areas of Concern. The RAPs are based on locally designed institutional frameworks. Their success in generating local involvement of stakeholder interests has been well documented (e.g., Hartig and Law 1994), and they provide some of the best examples of habitat restoration projects (Kelso and Hartig 1995).

Local land use

Local planning for land use is often the most critical arena for habitat loss or protection. Often from a local perspective, a particular development may seem to be a minor loss of habitat. The incremental loss of habitat, however, can become a major regional problem. The Sewell Report (the Commission on the Future of Planning in Ontario) is an example of major change in land-use planning that may be required to address this problem. The enabling legislation (Bill 163) contains a much stronger habitat protection focus based on a landscape approach to core natural areas, buffers and corridors, and wetlands. The bill calls for no development in these critical areas and for environmental impact statements in adjacent natural areas. The bill also provides for delegation of responsibilities to local municipalities in exchange for greater consistency of local plans with provincial policy. Although this trend of devolution of responsibility is a positive step, lack of funding to empower local municipalities to enhance planning may temper the outcome.

In Table 2, we provide examples of local projects affecting habitat. Of all the habitat restoration projects reviewed by Kelso and Hartig (1995), the restoration projects associated with the Thunder Bay Remedial Action Program stand out as successes in generating local involvement in habitat protection

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Table 2. Summary of projects involving habitat alteration within local jurisdictions.

Project	Type of habitat alteration	Circumstances and outcome
Cross Village, Michigan	Marina Development Project impacting 15 acres (1 acre = 0.405 ha) of Lake Michigan bottomland and removal of 1100 ft (1 ft = 0.3048 m) of natural shoreline	Significant local interest in harbor or marina development since 1880s. During application for permits in 1992, biological assessment showed an adverse effect on an endangered species, the piping plover. *Permit denied and habitat remains undeveloped.*
Waukegan River, Illinois (Project 122; Kelso and Hartig 1995)	Enhancement of riparian and instream habitat in an urban reach	Project arose as a joint venture of the Waukegan Park District, City of Waukegan, and the Illinois EPA to stabilize the Waukegan River and to prevent damage to sewer lines. Workshops for local interests were used to prepare for the project and extensive collaborations were involved in the planning, implementation, and monitoring of the restoration. *Project successful and used as template for similar projects in the area.*
Franklin Creek State Park, Illinois	Demonstration of enhancement of bank cover to enhance instream habitat for smallmouth bass	Project arose as a pilot project of the Illinois Department of Environmental Conservation. Project was not coordinated with local park management, but resulted in a successful habitat restoration. *Restoration was successful, but lack of involvement of local interests limited its transferability.*
Thunder Bay, Ontario (Projects 2–6 and 29; Kelso and Hartig 1995)	Various habitat restoration projects	Projects are components of the North Shore of Lake Superior Remedial Action Plans. Thunder Bay is one of four Areas of Concern on the north shore of Lake Superior. Habitat restoration projects involve coordination among Environment Canada, Great Lakes Cleanup Fund, Ontario Ministry of Natural Resources, and Ontario Ministry of Environment and Energy. Staff from these agencies share common offices to enhance coordination of restoration efforts. *Projects vary in attainment of restoration goals, but are highly successful in coordination of jurisdictions and in promoting local involvement.*

and restoration, in coordinating involvement of various governmental agencies, and in scope of activity. These successes may arise from a fortuitous match of scale of problems and size of the local communities. The Metropolitan Toronto RAP, for example, had to reduce its scale of operation to watershed units before effective planning could begin. A special feature of the Thunder Bay RAP, however, is the formation of a common staff from Environment Canada, Department of Fisheries and Oceans, Great Lakes Cleanup Fund, OMNR, and Ontario Ministry of Environment and Energy to support the Thunder Bay and other three Canadian RAPs in Lake Superior out of a single program office, the North Shore of Lake Superior RAPs. This common staff has proven adept at circumventing potential impediments that arise from variation in mandate and authority of the individual agencies that they represent.

The contrast between the Waukegan River and Franklin Creek State projects is also instructive. Both projects succeeded in restoring habitat, but the local involvement generated by the consultation process of the Waukegan River project had a more lasting impact on approach to stream restoration in the region and on park management. The contrasting emphasis on local responsibility in these two projects demonstrates substantial gain for investment in consultation with local stakeholders and managers. In addition, local responsibility generates local involvement and citizen observers, who can function as "watchdogs" for restoration efforts (e.g., The Bay Area Restoration Council, Hamilton Harbour). Local involvement in habitat protection, however, is not always so amicable. As was the case in the Cross Village example in Table 2, local development preferences may conflict with efforts to preserve habitat. In such cases, only laws such as the Endangered Species Act provide the basis to prevent habitat degradation.

Response of government agencies to habitat issues

Changing role of the IJC

The IJC has evolved in response to changing demands placed on it by government and others. Now, much of its work is focused on the responsibilities and powers assigned to it under the 1987 protocols (amendments to the 1978 GLWQA). In general, the IJC has adjusted to a more distant relationship with government agencies. The reduced input of government scientists and managers into the IJC process has been balanced by a much greater involvement of nongovernmental voices. The IJC's work tends to focus on a 2-yr cycle involving a major public conference followed by the preparation of a biennial report to the governments of Canada and the United States.

The IJC has continued to play a major role in encouraging and assessing the RAP commitments of the parties. Overall,

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however, the IJC's role as a coordinator–facilitator of work related to the GLWQA has diminished. These responsibilities with the 1987 protocols fall to the parties and their implementing agencies (U.S. EPA and Canada's Department of the Environment). Therefore, the IJC has begun to focus more attention of the "evaluation" role as its primary function under the GLWQA.

Changes in selected water quality agencies

U.S. Environmental Protection Agency

Change to an ecosystem focus within the EPA became evident in the 1990s with the writing of the Multi-Agency Great Lakes 5-Yr Strategy. The Strategy departed significantly from previous efforts by the EPA because it integrated water quality and habitat issues and was a multiagency, partnering effort. Many agencies and individuals now participate in binational partnerships. Significant developments in this regard include the Binational Program to Restore and Protect the Lake Superior Basin, the LaMPs, RAPs, the Lake Michigan Mass Balance study, the Great Lakes Water Quality Initiative, and the State-of-the-Lakes Ecosystem Conference (SOLEC).

Environment Canada

In 1993, various departments within the Ontario Region of Environment Canada reorganized into new branches. The reorganization was to streamline institutional arrangements and make more efficient use of personnel. From a wildlife habitat perspective, most responsibility now rests with the Environmental Conservation Branch, which consists of the Canadian Wildlife Research Management, Canadian Wildlife Science, Ecosystem Health, Restoration Programs, and Conservation Strategies Divisions. Much of the former Canadian Wildlife Service, Great Lakes Branch, is contained within this new branch. The Great Lakes Cleanup Fund, which finances most of the habitat rehabilitation projects, is in a different branch as is the Citizenship Division, which is responsible for involving the public in restoration activities. The new structure of the Ontario Region of Environment Canada raises some concerns. First, the reorganization continues to fragment responsibility for general habitat issues; raising doubt on its ability to deliver habitat protection and restoration. Second, reorganization of the Ontario Region does not alter other institutional arrangements. Coordination with other federal agencies is thus further complicated.

National Resource Conservation Service

The USDA has responsibility for the protection of highly erodible lands, wetland prairies, and streams. These federally funded programs are administered locally according to federal and state guidelines. The USDA effort is organized around County offices, which have boards of locally active landowners. These County offices receive funding and technical services from the Soil and Conservation Service and educational programs from the Co-operative Extension Service. Social conservation service projects for local landowners are reviewed by the Soil and Water Conservation District, which is a locally elected, state-funded board. Alternative funding programs are now emerging from an agricultural approach to ecosystem management.

Under a system of block grants to States for conservation practices, grassroots efforts have emerged to strike a balance between the economics of agriculture and protection of the environment. For example, a block grant proposal from the Heartland Water Resources Council asserts, "...the federal farm programs would function in a way that encourages production on land which is not floodprone, not highly erodible, nor at risk of ground water contamination." They propose to shift from an intrafarmstead to interfarmstead allocation of acreage set aside from production to meet requirements for federal assistance. Allowing farmers to swap land, which has been set aside from production, with production acres provides an opportunity to protect the best or most environmentally sensitive lands. Landowners with highly productive uplands can farm their set-aside acreage by buying certificates in acreage from landowners with flood prone wetlands or riparian acreage.

Changes in fishery agencies

With the 1980 signing of the Joint Strategic Plan for Management of Great Lakes Fisheries (SGLFMP), the provincial, state, and tribal fish management agencies moved to place their management in an ecosystem context (GLFC 1980). In adopting the strategic plan, fish managers were responding to a more holistic concern with the resources of the Great Lakes as exemplified by the ecosystem focus of the 1978 GLWQA. Although many elements of the SGLFMP were in place prior to 1980 (cf. Dochoda and Koonce 1994), promotion of common fish management policies for stocks of common concern by individual lake committees and requirements for planning and reporting were set forth that would track progress. The requirements of each lake committee were: (1) to develop a set of fish community objectives; (2) to specify of environmental objectives necessary to achieve the fish community objectives, and (3) to publish periodic state of the lake reports.

To assist the lake committees with formulation of environmental objectives, SGLFMP also created a Habitat Advisory Board, which could provide technical assistance on habitat issues and communicate the environmental objectives of fish managers to environmental management agencies and to advise them about the potential impacts of water quality management on fishery planning.

Discussion

Although empowerment of local interests seems to generate more fundamental change in habitat restoration, central government involvement also appears to be a necessary ingredient for successful projects. Provincial and federal agencies are repositories of technical assistance and funding that are vital to local initiatives. Where central government provides a source of guiding principles and general policy, local interests can devise effective implementation that makes sense in the local context. By this mechanism, central governments can insure value for funds invested and insure accountability to public policy and community values. Perhaps more fundamentally, central government has an important role as a memory for social commitments to environment protection and the ways of accomplishing these goals. Because they address a wide array of problem situations, central government agencies can act as a store of experience and source of information on approaches and networks.

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Whatever the level of government from which it emerges, public education on the benefits to individuals of good habitat management practices is essential. Much more habitat protection and restoration is possible through local landowners than through attention to large-scale habitat degradation. In many cases, large-scale degradation is the cumulative consequence of small-scale activities. Agricultural extension agents working within the context of Soil and Water Conservation Districts have proven to be extremely flexible and responsive at helping landowners find cost-effective ways of minimizing habitat damage. This type of educational outreach is a vital role of government.

Conclusions and recommendations

Present institutional arrangements tend to be impediments to habitat restoration and protection at scales necessary to effect ecosystem structure and function of the Great Lakes. In reaching this conclusion, we find that others have also noted that, despite some encouraging signs of progress, separation of water quality, water quantity, and resource management creates conflicting management actions, and these need to be unified (Hartig 1993; Koonce 1994*b*). Separate mandates for management agencies also affects the amount of normal coordination of national, regional, and local government programs. As Francis et. al. (1979) point out so well, the number of government organizations in various areas of responsibility increases dramatically from the federal to local levels. In such a mix of jurisdictional and management mandates, cooperation means loss of autonomy and potential compromise of an agency's responsibilities. Recognizing that habitat protection must occur at a local level and that partnerships are essential to successful restoration initiatives, we believe that the problem of institutional arrangements may have to be cast in a new perspective. The deal-making approach of indigenous peoples offers such an alternative approach. Based on principles of respect, equity, and empowerment, deal making succeeds when a balance is struck between rights and responsibilities of local autonomy.

Our recommendation, therefore, is that habitat protection in the Great Lakes seek a different orientation. To protect and restore habitat, governments should empower and support local communities to take responsibility for the environment. There is both promise and peril in this recommendation. Of greatest concern are failures when local interests do not act responsibly. To guard against such failures requires a few guiding principles. First, government should begin to assume a new role. Empowerment of local interests should be the goal from the start. By working with local resource people and assisting local organizations, government can encourage responsible behavior and promote habitat protection and restoration that is meaningful at the scale of ecosystems of the Great Lakes. In this new role, government would provide technical assistance, funding, be a source of guiding principles and policy, insure value for money invested, and provide social memory and store of experience. Much of the infrastructure necessary to implement this approach is in place with existing networks of agricultural representatives, extension agents, and urban county planning or coordinating agencies. More than fish and wildlife benefits accrue from good habitat management practices. By empowering available local interests and people and building on existing infrastructures, institutional arrangements become less of a problem.

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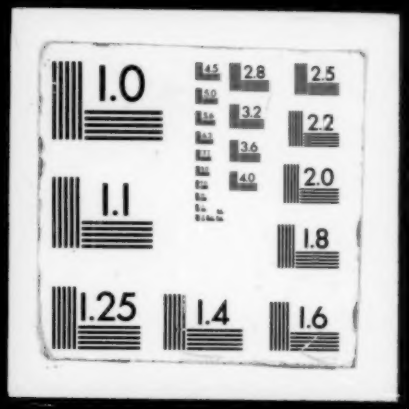
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